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Evaluation of Macroinvertebrates as a Food Resource in the Assessment of Lotic Salmonid Habitat

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EVALUATION OF MACROINVERTEBRATES AS A FOOD RESOURCE IN THE ASSESSMENT OF LOTIC SALMONID HABITAT

by

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ABSTRACT

Evaluation of Macroinvertebrates as a Food Resource in the Assessment of Lotic Salmonid Habitat

by

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Criteria used to characterize lotic salmonid habitat are often based on observed correlations between physical habitat characteristics and salmonid abundances. A focus on physical habitat features ignores other habitat components, such as an adequate supply of food that set the physiological limitations on salmonid growth and survival. This study outlines the development of a habitat assessment approach that focuses on how invertebrate food availability interacts with stream temperatures to determine salmonid growth potentials. Abundances of benthic and drifting invertebrate communities, stream temperatures, and juvenile steelhead trout (*Onchorhynchus mykiss gairdneri*) summer growth rates and abundances were measured within 10 distinct stream segments in central Oregon. Stream temperatures and growth rates were used as inputs for bioenergetics model simulations to produce estimates of *O. mykiss* summer consumption rates. Measures of invertebrates providing the best description of food availability were chosen based on their ability to explain

observed variation in salmonid consumption. Much of the variation in *O. mykiss* consumption estimates was explained by measurements of total drift biomass along a type II predator response curve. A random effects analysis of variance (ANOVA) was used to partition variation in invertebrate abundances across spatial and temporal scales. Quantification of variation at multiple scales allowed identification of a relevant spatial scale at which to assess macroinvertebrates relevant to salmonid populations, and compare the precision associated with measures of benthic and drifting invertebrate abundances. Results suggested that spatial variation in drifting and benthic invertebrate abundances are greatest at the scale of streams. Total drift biomass and total benthic biomass were more precise at the stream and stream reach scale than drift and benthic density. The information provided by this study will be used to guide the development of sampling approaches that describe invertebrates in a manner more directly related to salmonid production.

(126 pages)

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CHAPTER 1

INTRODUCTION

For fish, habitat represents a place that contains the biotic and abiotic components necessary for reproduction, growth, and survival. Understanding the causative relationships between habitat processes and salmonid production will allow us to better predict how salmonid populations will respond to environmental change. A common paradigm in the study of how habitat processes may be limiting to salmonid production has been to focus on physical habitat features (Rosenfeld 2003). In addition to the requisite physical components, habitat must also contain the food resources necessary to support the growth and survival of salmonids. Unfortunately, food resources are rarely evaluated as part of habitat monitoring and assessment programs (Fausch et al. 1988). Several factors may have acted as a deterrent for using invertebrate food resources to describe the quality of salmonid environments. First, because salmonid production is an integrated response to a number of environmental conditions, a direct relationship between food abundance and salmonid production can be difficult to detect (Folt et al. 1998). Second, stream invertebrates, the primary food resource for salmonids, can be extremely variable across space and time (Resh et al. 1988). This variability makes accurate quantification of invertebrate abundances difficult, and also creates uncertainties for researchers and managers regarding the relevant spatial and temporal scales over which invertebrates should be monitored as a salmonid food resource.

The following study was designed in an attempt to overcome some of these difficulties. This study takes an in depth look at stream macroinvertebrate community characteristics in relation to the vital rates and abundances of juvenile steelhead trout (*Onchorhynchus mykiss gairdneri*) populations. Ideally, the information gained from this study will aid in the development of macroinvertebrate sampling approaches that can be used by researchers and managers to assess this often overlooked habitat component. In addition, the results of this study are meant to further the understanding of how invertebrate food abundances affect the production of lotic salmonid populations.

Background and impetus for this study

Food limitations to lotic salmonid production

It comes as a surprise that invertebrate food abundances are rarely evaluated as part of salmonid habitat monitoring and assessment programs, as interactions between lotic salmonids and macroinvertebrate communities are well studied. However, from these studies, various lines of evidence have both supported and detracted from the concept that food abundance is an important driver of lotic salmonid population dynamics. In some cases, experimental studies focusing on the ability of salmonid predators to deplete macroinvertebrate community abundances in stream environments have yielded ambiguous results (Cooper et al. 1990). For example, in a manipulative study, Allan (1982) showed that reducing trout densities in stream enclosures had no effect on invertebrate community abundances. This would imply that salmonids consume only a

fraction of the food resources in their environment, and suggests that food is often in excess of salmonid consumption. To a greater extent, studies of salmonid-invertebrate interactions tend to support food limitation in lotic salmonid populations. For instance, Boss and Richardson (2002) found that increasing food abundances above ambient levels increased the growth and survival of Cutthroat trout (*Oncorhynchus clarki*). Support for bottom-up limitations to salmonid production are found in experiments that have documented increases in invertebrate and salmonid secondary production as primary production is experimentally increased through nutrient additions (Deegan and Peterson 1992). In addition, a number of studies have documented positive correlations between invertebrate abundances and salmonid demographic rates (Cada et al. 1987; Elliott 1973; Filbert and Hawkins 1995; Nislow et al. 1998; Wilzbach and Cummins 1986).

Despite this evidence, predicting how salmonid populations will respond to variation in food resource abundance remains a difficult task (Hayes et al. 1996). The majority of studies attempting to quantify the importance of food availability rely on the documentation of correlations between measures of fish abundance (density) or performance (growth) and variation in invertebrate abundances (Rosenfeld 2003). These types of studies lack the ability to account for ecological and physiological interactions that will ultimately determine how individuals or populations of salmonids will respond to variation in food abundance.

Relating food abundance to salmonid production

If food is indeed limiting to salmonids, calling on some basic tenants of ecology can assist us in envisioning how variation in this limited resource may affect salmonid populations. The basic Ideal Free Distribution (IFD) described by Fretwell and Lucas (1970) would predict that habitats with greater food resource availability would exhibit higher predator densities. Under IFD, predators will choose to occupy the highest quality habitat to maximize their energetic gains. However, as predator densities increase, per capita energy gains will decrease until it is more profitable for some individuals to occupy lower quality habitat. IFD predicts that if food is limiting, habitats with greater food resources can support higher predator densities. However, fish will distribute among patches that differ in quality so that consumption remains constant. This simple model of how food abundance may structure salmonid population densities can be seen in a study by Keeley and Grant (1995), who were able to explain differences in juvenile Atlantic salmon (*Salmo salar*) population densities as a function of food abundance. In this case, the differences in density were thought to be attributable to relaxation of territory size requirements in habitats featuring greater food abundances.

Indeed, IFD theory would predict that for food limited populations, territory size requirements would follow an inverse relationship with food abundance. However, strict IFD theory, in which competitors have equal competitive ability is in many cases is an over simplification, and factors beyond resource abundance interact to determine individual space requirements (Chapman 1966). For lotic

salmonids, competitive ability and territory size have been shown to increase with body size (Keeley 2001). For example, Keeley (2003) demonstrated that the density of surviving juvenile Steelhead trout (*Oncorhynchus myk*iss) in experimental tanks under controlled food rations followed an inverse relationship with individual body mass. Observational field studies of juvenile Atlantic salmon have demonstrated similar patterns of survival and body size (Steingrimsson and Grant 1999). These observations deviate from the traditional IFD framework, suggesting greater resource acquisition for superior competitors (Holmgren 1995). In this case, the response to greater food abundance would not consist exclusively of greater densities, but also increased individual growth for superior competitors. Thus, individual growth should also be considered when evaluating how a population of fish may respond to variation in food abundance. However, growth for salmonids is fundamentally tied to stream temperatures. Thus, in order to isolate the contribution that food abundance has on salmonid growth, one must also consider how temperature drives salmonid metabolic rates to determine growth.

Salmonids are ectotherms, and their metabolic rates and processes operate as a function of ambient stream temperature (Elliot 1982). Rates of digestion and absorption increase with temperature, ultimately governing the rate of maximum consumption. While temperature controls maximum energetic gains, it also controls energetic costs, as basal metabolism increases with temperature. However, except at very high temperatures, the maximum rate of consumption (potential gains) increases with temperature faster than increases in

energetic costs. Thus, at high temperatures salmonid growth potentials is generally greater, provided that an adequate supply of food exists to satisfy increased metabolic demands.

These nonlinear relationships between fish metabolic rates and temperatures mean that fish fed at identical rations in contrasting temperatures will exhibit different growth rates. Thus, any correlations between food abundance and salmonid growth observed in the field have the potential to be confounded by stream temperatures. Another layer of complexity is added when the size structure of fish populations is considered. Fish metabolic rates scale allometrically with body size (Jobling 1994). From this, different growth rates can be expected for fish of variable sizes when feeding at identical rations even when temperatures are constant (Elliot 1982).

Based on these interactions it becomes difficult to isolate the contribution that food abundance has on growth for size-structured populations of fish across a gradients of temperatures. Fish bioenergetics models have emerged as a tool for quantifying the mechanistic relationships between environmental conditions and fish growth rates (Nakano and Nakamura 2006; Ney 1990). Bioenergetics models are based on the understanding of how consumed energy is partitioned between metabolism and growth according to the effects of temperature and fish size (Hanson et al. 1997). The model is based on a simple energy budget equation of the form:

$$\text{consumption} = \text{growth} + \text{metabolism} + \text{waste losses}$$

where *growth* is the surplus energy allocated to somatic or gonadal growth, *metabolism* is the total energetic cost of metabolic work (standard metabolism, digestion, activity), and *waste losses* include the sum of energy lost through processes of excretion and egestion (Hanson et al. 1997). Thus, bioenergetics models are often used to quantify the energetic costs and benefits associated with the temperature regimes that fish inhabit (Rosenfeld 2003).

Bioenergetics models are also commonly used to study how environmental characteristics function to limit prey acquisition (Brandt et al. 1992; Dieterman et al. 2004; Krohn et al. 1997; Meka and Margraf 2007). For logistical reasons, it is notoriously difficult to quantify the consumption rates of *in situ* fish populations, as it requires intensive field sampling (Hartman and Hayward 2007). However, because bioenergetics models are based on a budget in which energetic gains must equal losses, differencing can be used to solve for consumption when growth and temperature information are available. From this, bioenergetics models have facilitated the study of how environmental features may function to limit fish consumption.

Invertebrate production and availability

The potential food supply for salmonids depends on processes occurring at multiple temporal and spatial scales. Processes occurring both within the stream channel, and in the surrounding riparian area control macroinvertebrate production (Baxter et al. 2005; Poff and Huryn 1998). At the landscape scale, regional climate patterns drive stream temperatures, dictating the metabolism

and growth of stream invertebrates (Huryn and Wallace 2000). At the watershed scale, variation in riparian composition and geology will directly or indirectly affect invertebrate production. Limits to thermal exposure set by canopy cover, and the regulation of ground water infiltration by geology further control stream temperatures. At the reach scale riparian vegetation influences the quantity and quality of food available for invertebrate primary consumers (Murphy et al. 1981).

While it is well understood that invertebrate community composition and abundance varies among stream environments, what is less well described is if greater invertebrate production necessarily results in increased prey availability for salmonids? While salmonids may occasionally forage epibenthically (Angradi and Griffith 1990; Nislow et al. 1998; Tippets and Moyle 1978), foraging is primarily focused on invertebrates that are drifting in the water column (Angradi and Griffith 1990; Cada et al. 1987; Dedual and Collier 1995; Elliott 1970). However, studies of invertebrate community dynamics have demonstrated that the proportion of invertebrates occurring in the drift at any time amounts to only a fraction of the total benthic community (Elliot 1967). This is not surprising, as the propensity for invertebrates to occupy the drift depends on a variety of morphological, behavioral, and/or micro-habitat utilization differences among taxa (Billy et al. 2002; Rader 1997). For instance, invertebrates occupying hyporheic habitats exhibit a low probability of becoming dislodged in the current and consumed by salmonids. In contrast, invertebrates occupying erosional substrates may have a higher likelihood of becoming dislodged into the water

column. Specific taxa also enter the drift according to behavioral cues as a means of dispersal or during adult emergence (Allan 1987). These observations suggest that increased invertebrate production does not necessarily equal a proportional increase in salmonid food availability (Poff and Huryn 1998).

Macroinvertebrate monitoring in streams

Macroinvertebrates communities have been evaluated in the assessment of aquatic environments since the early 1900's, and today invertebrates have become the most widely collected biological indicator of freshwater resource health (Bonada et al. 2006). A number of characteristics make macroinvertebrate assemblages an ideal group of organisms for bioassessment purposes. They are ubiquitous and speciose across freshwater environments. Macroinvertebrate taxonomy and life-history characteristics have been well described for many regions. Many species are also sensitive to pollution and habitat alterations caused by human activities (Fore et al. 1996). Because of these characteristics, species composition is often used to describe the impairment of freshwater habitat. This approach relies on empirically derived relationships between metrics of macroinvertebrate assemblage structure (e.g. species richness, number of predator species) and reference habitat conditions (Karr 1991). The degree that observed macroinvertebrate species composition differs from expected values is used to estimate the degree that a stream has deviated from reference conditions. These types of assessment are commonly collected to provide an indirect measure of habitat quality for salmonids. However, a mechanistic link between invertebrate bioassessment information

and limitations to salmonid production has not been established. Because macroinvertebrates represent the primary source of food for salmonids, a method to interpret invertebrate information as prey may prove to be a more relevant indicator of salmonid habitat production potential.

Federal monitoring for Pacific salmonids

Human activities directly or indirectly affect salmonid populations across all life-history stages, resulting in the precipitous decline of salmonid abundances in the northwestern United States (Nehlsen et al. 1991). Currently, 26 Evolutionary Significant Units of Pacific salmonids are federally listed as threatened or endangered under the Endangered Species Act (ESA). Much of the cause for these large declines is attributable to the degradation of freshwater spawning and rearing habitat (Kareiva et al. 2000).

As mandated by the ESA, the Federal Research Monitoring and Evaluation (RME) program has the goal of describing the “health” of fish population processes and habitat. This information will be used to determine if current land management and mitigation measures should be altered to ensure the future persistence of Pacific salmonids. These assessments will also be used to prioritize areas for restoration activities that will improve upon habitat conditions that may be limiting to salmonid production. Finally, the RME program seeks to assess the degree that restoration actions are achieving their goals. NOAA Fisheries launched the Integrated Status and Effective Monitoring Program (ISEMP) in 2003. The ISEMP is tasked with determining the most efficient means of meeting the goals of federal RME for Pacific salmonids under

the ESA. To this end, ISEMP objectives include testing the accuracy and precision of information collected by monitoring protocols, and identifying novel indicators that describe causal relationships between habitat features and fish population processes.

Statement of research objectives

The following two chapters of this document describe the research I conducted during pursuit of a Masters of Science in Aquatic Ecology at Utah State University. Each chapter was written as a stand-alone work, intended to be published as a separate peer review journal article. However, each chapter complements the other by meeting one of two broad objectives under the larger goal of developing sampling approaches for monitoring salmonid food availability.

The first chapter is entitled “Spatial and temporal variation in lotic macroinvertebrate community abundances: relevancy to stream habitat monitoring programs.” In this chapter I focus on describing the temporal and spatial variation of indicator metrics, which in the case of this study are measures of invertebrate abundances. Using a multi-scale survey design, this section of my thesis research sought to identify an appropriate scale over which invertebrate food abundances should be assessed as food for lotic salmonids. Further, the data collected in this chapter also provided a means to test the accuracy and precision of sampling designs and methodologies that will be used to describe invertebrate food availability. The second chapter is titled “Summer growth of juvenile Steelhead trout (*Onchorhynchus mykiss gairdneri*) in relation

to food abundance and temperature." In this chapter I sought to establish the relevancy for monitoring food availability by establishing causal relationships between invertebrate community abundances and salmonid growth rates.

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CHAPTER 2

SPATIAL AND TEMPORAL VARIATION IN LOTIC MACROINVERTEBRATE ABUNDANCES: RELEVANCY TO STREAM MONITORING

Abstract

The ubiquity of stream macroinvertebrates, coupled with their responsiveness to environmental gradients, has lead stream monitoring and assessment programs to evaluate invertebrate community composition as indicators of water quality. Because of this, research has been devoted to identifying the spatial scales at which invertebrate community composition responds to environmental heterogeneity. Throughout the Pacific Northwest monitoring programs are being developed to evaluate factors affecting freshwater production of anadromous salmonids. Stream macroinvertebrates function as the primary source of prey for juvenile and adult salmonids that occupy stream systems. Thus, identifying variation in stream invertebrate communities can also aid in the development of sampling protocols that describe invertebrate food availability for salmonids. In lotic environments, salmonids are thought to primarily forage on invertebrates drifting in the water column. Unfortunately, stream monitoring and assessment programs rarely collect invertebrate drift samples. This study utilizes an extensive set of invertebrate drift and benthic samples collected throughout 6 Oregon streams using a multi-scale survey design to describe variation in invertebrate abundances. A random effects analysis of variance (ANOVA) was used to partition components of variation in

measures of invertebrate abundances across spatial as well as temporal scales. Quantification of variation at multiple scales allowed identification of a relevant spatial scale at which to assess macroinvertebrates as they function as a food resource for salmonid populations, and compare the sampling precision associated with various measures of benthic and drifting invertebrate abundances. This study also sought to establish associations between drifting and benthic invertebrate community abundances. Linkages between benthic and drifting invertebrate sampling would allow past and future benthic invertebrate monitoring information to be interpreted as food availability for drift feeding salmonids.

Results of this study suggest that spatial variation in abundances of drifting and benthic invertebrate communities tends to be greatest at the scale of whole streams. Variation among streams was generally greater than the sum of additional sources of spatial and temporal variation occurring within streams. Measures of total drift biomass and total benthic biomass were more precise at the stream and stream reach scale than measures of drift density and benthic density. In the streams surveyed, drift sample abundances were positively correlated with benthic invertebrate sample abundances. Ideally, the information provided by this study will be used to guide the development of sampling approaches and methodologies that accurately describe invertebrates in a manner more directly related to salmonid production.

Introduction

Ecologists have long recognized that variation in the physical, biological, and chemical components of natural systems occurs along multiple spatial and temporal scales of organization (Wiens 1989; Poff 1997; Poff and Huryn 1998; Durance et al. 2006). The degree that organisms respond to gradients in environmental variation occurring at multiple scales governs organism distribution, and determines community composition (Downes et al. 1993; Palmer and Poff 1997). Identifying the scale at which organisms and environmental characteristics exhibit and respond to variation is of fundamental importance to the study and understanding of ecological interactions (Wiens 1989). Ecological research and environmental assessments may be confounded through the employment of sampling designs that collect information at a scale that does not capture variation in the process or pattern of interest (Palmer and Poff 1997; Folt et al. 1998). This lends importance to studies that describe environmental and organismal heterogeneity using a multi-scaled framework. Ecological studies of this type provide information that can be used to remedy the mismatch between sampling design and ecological process that are attributable to scale inconsistencies (Cooper et al. 1997). For example, Nislow (1998) found that stream salmonid performance (foraging rate) tended to track flow variation and invertebrate prey availability at large spatial scales among streams rather than among smaller spatial scales within streams or stream segments. Thus, studies conducted at small spatial scales would overlook the importance of these habitat characteristics as determinates of lotic salmonid production.

Stream macroinvertebrate assemblages are influenced by variation in biotic and abiotic processes at a number of spatial and temporal scales (Downes et al. 1995; Boyero 2003; Parsons et al. 2003; Heino et al. 2004). For example, variation in stream temperature, discharge, nutrient availability, and the composition of riparian vegetation all act to influence the distribution of stream macroinvertebrates. These features of stream environments are determined at regional scales by climatic conditions, and at the catchment or watershed scale by elevation, drainage area, and geology (Whittier et al. 1988). At the scale of streams or stream segments, riparian vegetation controls the infiltration of sunlight and introduction of allochthonous materials that further influence macroinvertebrate assemblage structure (Hawkins and Sedell 1981).

The ubiquity of stream macroinvertebrates, coupled with their responsiveness to environmental gradients, has lead to the development of stream monitoring programs that evaluate invertebrate community composition as an indicator of water quality. Because of this, much research has been devoted to identifying the spatial scales at which invertebrate community composition responds to environmental heterogeneity (Bonada et al. 2006). In the Pacific Northwest, monitoring programs are currently being designed to evaluate factors affecting freshwater production of anadromous salmonids. Stream macroinvertebrates function as the primary source of prey for juvenile and adult salmonids that occupy stream systems (Elliott 1973; Allan 1978). Thus, information describing variation in stream invertebrate communities can

also be used to aid in the development of sampling protocols that describe invertebrate food availability for salmonids.

The research presented in this study was designed to meet two objectives under a larger goal of developing approaches for sampling invertebrate food availability for lotic salmonids. First, a multi-scaled sampling approach was taken to describe variation in measures of invertebrate community abundances across spatial as well as temporal scales. Comparing the relative magnitudes of variation in invertebrate abundances across time and space allowed for the identification of a most appropriate and feasible scales at which to monitor invertebrates as a proximate measure of salmonid food abundance. This approach also provided information that was used to determine if stream invertebrate abundances can be characterized at a spatial scale relevant to salmonid populations (e.g., stream, reach, or segment) with a modest amount of sampling effort.

A second study objective sought to determine if simple associations between drift and benthic sampling abundances can be established. Much research suggests that macroinvertebrates entrained in the water column function as the primary source of forage for lotic salmonids, and that invertebrate drift samples provide the most descriptive measure of salmonid food availability (Elliott 1973; Nislow et al. 1998; Romaniszyn et al. 2007). While invertebrate information is collected by many salmonid habitat monitoring programs, this sampling is aimed at the assessment of water quality, and usually does not include samples of invertebrate drift. More commonly, samples are collected

using kick-net or surber type sampling gear. These types of sampling gears are limited to describing abundances of benthic invertebrates occupying the stream substrate (Bonada et al. 2006). Thus, the second objective of this study sought to develop simple relationships between drifting and benthic macroinvertebrate sample collections. Development of these relationships would allow information more directly related to salmonid production to be gleaned from past and future benthic invertebrate monitoring information.

Study area and methods

Study area

This study was conducted in several high-desert tributary streams in the John Day River Basin in central Oregon. These streams provide important spawning and rearing habitat for both anadromous and resident populations of steelhead trout (*Oncorhnchus mykiss gairdnerii*). Sampling reaches were selected based on geomorphic and valley characteristics in order to encompass a diversity of stream conditions. Three distinct sampling reaches were established on each of Murderers and Black Canyon Creeks, and one on Deer Creek, tributaries of the South Fork of the John Day River. Reaches located on the same stream were separated by roughly 2 km in stream distance. Three additional study reaches were established in the Bridge Creek sub-basin of the John Day River. Here, one study reach was selected on each of Bridge Creek, Bear Creek, and Gable Creek (Fig. 2.1).

Macroinvertebrate sampling

Field sampling occurred throughout the summer of 2006, between mid-June and mid-August. Two separate sets of drift sample collections were used to describe characteristics of invertebrate drift communities. The first set of samples was used to describe fine scale spatial and temporal variation in drift abundances occurring between habitat units and across several days, relative to variation among streams and stream reaches. This set of samples was collected over a short time period between the dates of June 15 and June 25. All drift samples were collected between 1200 and 1700 h. As flows were relatively high during June, drift sample durations were limited to between 2 and 4 h to avoid net clogging. On each date, two drift nets were set simultaneously at three fast-water habitat units (riffles) separated by greater than 100 m. This was then repeated over three consecutive days at a single study reach on Murderers Creek, Black Canyon Creek, and Deer Creek. To better describe variation among streams and reaches, one riffle section was sampled using two nets on a single date at two additional reaches each on Murderers Creek and Black Canyon Creek (Appendix, Table A.1, Fig. A.1).

A second set of drift samples was used to describe larger scale temporal variation in invertebrate drift abundances occurring over several months, in relation to variation among streams and among stream reaches. This sampling utilized drift samples collected over entire 24 h periods at each of the 10 reaches. Drift nets were replaced at roughly 8 h intervals to avoid clogging. This sampling occurred on either two or three sampling dates between early July and late

August. On one date at three reaches, drift nets were replaced at roughly 3 h intervals to allow a finer description of the diel periodicity in invertebrate drift abundances (Appendix, Table A.2, Fig. A.2).

Drift nets had a mouth opening of 40 cm in height and 20 cm in width, and were composed of 1 mm Nitex® mesh. Each drift sample collection consisted of anchoring two nets along a cross-section of the stream channel with the net mouth oriented perpendicular to stream flow. Nets were usually near the thalweg in order to sample a maximum amount of the total stream discharge. The top of the net mouth was always protruding above the surface of the water to capture terrestrial and emerging aquatic invertebrates, the bottom was suspended roughly 2 cm above the channel substrate to prevent invertebrates from crawling into the net. Total volume of flow sampled was estimated by multiplying the average of velocity measurements recorded at the center of the net mouth just after setting and just before removing each net, by the area of the net mouth submerged, by the total time a net was deployed (Allan and Russek 1985).

Benthic invertebrate samples were collected in the same riffle habitat segments as our drift collections. At three reaches, samples were collected at three separate fast-water habitat units separated by 100 m in linear stream distance. Benthic samples were collected from only one riffle section at the seven additional reaches. This sampling design was repeated on two dates at each reach between late June and mid-August (see Appendix). Sampling dates at each reach were separated by intervals ranging between two to four weeks.

Benthic macroinvertebrate samples were collected using a 500μm Nitex® mesh surber-net that samples a fixed area of 0.09 m^2. Each benthic sample was collected by disturbing the substrate enclosed by the surber-net in eight randomly selected locations in each fast-water habitat section. Each of the eight surber sampler collections were pooled and treated as a single fast-water habitat sample.

Both drift and benthic samples were preserved in 70% ethanol in the field prior to being transported to the lab for processing. Following sorting, invertebrates in drift and benthic samples were counted and weighed according to taxa, life-history stage, and terrestrial or aquatic origin (Merritt and Cummins 1984). Aquatic larvae were grouped according to five major orders; Coleoptera, Diptera, Ephemeroptera, Plecoptera, and Trichoptera. Aquatic larvae not belonging to these orders were counted and weighed separately, and generally accounted for a small percentage of the total sample count and weight. Drift samples were partitioned into two additional groups consisting of emergent adult stages of aquatic invertebrates and terrestrial invertebrates. Each group partition was weighed after being placed in a drying oven at 60 C^o for a minimum 24 h period, or until samples had reached a constant weight. Dry weight was measured to the nearest 1 mg and adjusted for weight losses due to preservation using own unpublished regressions.

The total density (count) and biomass of drifting invertebrates per volume of water sampled was calculated for each drift net at each sampling event.

Benthic invertebrate density and biomass per area of stream sampled was calculated for each invertebrate grouping and for total invertebrate abundances.

Variation in drift and benthic abundances

A series of random effects ANOVA models were used to estimate and compare the magnitude of variance associated with invertebrate drift and benthic abundances across spatial and temporal scales. Only variation in total drift density and biomass were analyzed as different taxa of invertebrates in the drift are likely equally vulnerable as prey for drift feeding fish. Spatial and temporal factors in these models were treated as random effects because the response of interest was in variances instead of means (Bennington and Thayne 1994; Littell et al. 1996). Variance estimates produced by random effects ANOVA models were used to calculate the percent of variation in measures of invertebrate abundance attributable to each spatial and temporal scale. Variance estimates were also used to calculate signal-to-noise ratios. In many salmonid monitoring programs, stream attributes are characterized at the spatial scale of streams or stream reaches. Thus, in the calculation of signal-to-noise ratios the sampling "signal" is referred to as variance among reaches or streams, and sampling "noise" is any additional sources of within-reach variance (Kaufmann et al. 1999).

Separate random effects ANOVA models were used to estimate variance components in measures of drift density and biomass for each of the two sets of drift samples (i.e. short duration 2 h and 24 h drift sample collections). The first set of drift samples estimated variance among streams, among reaches, between riffles within reaches, from day-to-day, and between replicate drift nets.

Reaches were treated as a nested factor within streams, and riffles were nested within reaches within streams. Days were not crossed or nested within any other factors. Residual error in these models was interpreted as variation between nets. In this analysis, values of drift density and biomass were natural log transformed in order to meet ANOVA assumptions of heteroschedasticity and normality of errors.

The second set of 24 h drift samples estimated variance among streams, among reaches, and at the larger temporal scale of months. Reaches were nested within streams, and months were not nested or crossed with any other factors. Residual variation in this model was attributed to variance among nets. Analysis of untransformed data met standard ANOVA assumptions.

The distribution of variance in benthic abundances was estimated using a similar set of random effects ANOVA models. In addition to total benthic density and biomass, the variance associated with each major order of aquatic invertebrates described above was also evaluated. The layout for benthic sample ANOVA models estimated variance among streams, among reaches (within streams), and among riffles (within reaches). Because replication was on the two sampling dates, residual variation was interpreted as being due to changes in abundances across time (roughly two month). However, it is possible that the residual variation in this model may contain other sources of sampling variability not accounted for in this sampling design (e.g. variation within riffle habitats). Both total benthic density and biomass met standard ANOVA

assumptions when analyzed using untransformed values. Models treating each taxonomic group were natural-log transformed.

The additive nature of ANOVA models allows for the calculation of percent variation attributable to each temporal and spatial factor by dividing the variance estimate for each factor by the total variance present in the data set (Zar 1999). Signal-to-noise ratios were calculated according to two scenarios. The first treated the 'signal' as the total variance among the 10 sample reaches. Total among reach variance was estimated by replacing the factors in random effects models for *streams* and *reaches within streams* with a single factor representing each reach. The second scenario treated the 'signal' of interest as variance among the 6 streams, and was estimated by removing the factor for *reaches within streams* from random effects models. From this, signal-to-noise ratios were calculated as the ratio of the variance representing the 'signal' for each scenario to the sum of additional sources of variation. Percent variation and signal-to-noise ratios were calculated for each set of drift sample (2 h and 24 h) and benthic sample data.

A cursory look at the distribution of variances estimated using ANOVA models suggested that a considerable portion of the variance in total drift density and biomass was due to between net differences in invertebrate abundances. Thus, the potential to alleviate some of this variation was investigated by pooling information from channel replicate drift nets, much in the same way benthic surber sub-samples are pooled to create a single composite sample. To do this, drift density and biomass were recalculated based on pooling the total volume of

water and the total count or weight of organisms sampled by each net. Random effects models were then used to recalculate signal-to-noise ratios for the pooled drift datasets and compared to the results of the original analysis. Any increase in signal-to-noise ratios would indicate that pooling information from replicate drift sample collections can be used to decrease within-reach variance.

Sampling effort

Within-reach variance estimates from random effects models were included in a series of power analyses to estimate the amount of sampling effort necessary to detect differences or changes in mean invertebrate abundances among stream reaches. These power analyses used within reach sampling standard deviations estimated by random effects models. This analysis calculated the number of samples necessary to detect 25%, 50%, and 100% differences in the mean of total drift and benthic density and biomass using a t-test. Percent differences in abundance were calculated relative to the grand mean of each metric so that the results of the power analysis would be applicable over ranges of values that may be typically observed. Variance estimates used in the power analyses for drift sampling were taken from random effects models for pooled 24 h drift samples.

For each sample estimate, the probability of type I error (α) was set at 0.1. The sample size necessary to meet a level of statistical power (β) from 0.2 to 0.9 was calculated at intervals of 0.1. Because this often resulted in sample size estimates that are fractions, power was adjusted to meet estimated sample sizes

rounded to the nearest whole number. Sample sizes are presented as the number of samples collections per reach.

Transferability of sampling methods

Simple linear regression was used to assess the strength of the relationship between total drifting and benthic abundances. These regression models treated benthic density and biomass as independent variables, and 24 h drift density and biomass as dependent variables. Each observation in the regression models consisted of paired 24 h drift and benthic samples that had been collected on the same date at the same location (n=20). All variables and residual values were determined to meet standard regression assumptions.

Results

Variation in drift abundance

Drift samples collected across reaches at roughly intervals over a 24 h period demonstrated the extremes over which drift abundance can vary throughout the course of a single day (Fig. 2.2). Drift abundances were low during daylight hours. Values of drift density ranged between 5 and 25 no./100m^3, and drift biomass ranged between 5 and 20 mg/100m^3. At each reach, drift density and biomass appeared to peak either at sunset (between 2000 and 2200 h), or during the night (from 2200 to 0400 h). Drift abundances during sunrise (0400 to 0600) were also greater than those observed during the day.

The set of 2 h drift sample collections allowed comparison of the magnitude of variation in drift biomass and density among streams and stream reaches with variation between riffles, nets, and across consecutive days. In this set of drift samples the majority of variation in drift density and biomass was due to differences between streams (Fig. 2.3). Variation between reaches nested within streams accounted for only 2% and 10% of sampling variation in drift biomass and density, respectively. Within-reach variation between riffle habitat units was generally low, accounting for only 14% of the total variation in samples of drift density, and 11% in samples of biomass. No variation was estimated for drift density or biomass between consecutive days. Sampling variance between replicate nets accounted for 16% of the total variation in samples of total drift density as well as total drift biomass.

In the set of 24 h drift samples collected monthly, roughly 70% of the total variation in drift biomass and density was due to among-stream differences (Fig. 2.4). No variation between sampling reaches nested within streams was estimated by the model for samples of either total drift density or biomass. Temporal variation in total drift abundances across months was also low. Models estimated that 4% of the total variation in samples of drift density was attributable to differences among months. No variation between months was estimated for samples of drift biomass. Variation between nets accounted for roughly 25% of the total sample variance for measures of total drift density and biomass.

Signal-to-noise ratios (S:N) among streams were always greater than S:N among reaches for both total drift density and biomass. Measures of drift

biomass generally had greater S:N ratios than drift density (Table 2.3). For the set of 2 h drift sample collections, the ratio of among-stream variance to variance between riffles and across consecutive days was 2.76 for drift density and 2.91 for drift biomass. The ratio of variance among streams to variance across months and within streams (among reaches) for 24 h drift sample collections was 2.4 for drift density and 2.67 for drift biomass. Pooling information from replicate drift nets always increased S:N. For example, pooling of replicate drift nets increased 24 h drift sample S:N among streams from a value of 2.67 to a value of 7.2 for drift biomass. For drift density, S:N among streams increased from a value of 1.8 to a value 5.08 as a result of pooling information from replicate drift nets.

Variation in benthic abundance

Roughly 40% of the variation in total benthic biomass was due to among-stream differences, and 24% percent was due to differences among reaches within streams (Fig. 2.5). The benthic invertebrate sampling design was unable to detect variation among streams or stream reaches for measures of total benthic density. Only 9% of the total variance associated with total benthic biomass was attributable to differences between riffles, and 36% of the variance in total benthic density was attributable to differences in riffles. Residual variation, which was interpreted as variation across months, accounted for 64% and 27% of the total variance in benthic density and biomass, respectively.

The distribution of variance across scales varied for benthic samples varied considerably for each of the orders of aquatic invertebrates that were

evaluated (Table 2.2). Only Diptera density and biomass featured a large among stream variance component. Samples of Trichoptera biomass featured a large amount of variance among streams. All of the total variance in the density and biomass of Ephemeroptera and Plecoptera larvae was due to within-reach variance components of riffles and months.

In general, signal-to-noise ratios for most of the major orders of benthic invertebrates evaluated were low (<1) both among streams and among stream reaches (Table 2.3). Exceptions to this include the S:N among streams for Diptera density which was 1.36, and S:N for Trichoptera biomass which was 2.86 among streams and 3.92 among reaches. The S:N for total benthic biomass was 1.34 among reaches. Total benthic biomass featured a large signal among streams with a value of 6.38.

Sampling effort

Power analyses demonstrated that when among-reach differences in drift abundance are large, statistically powerful tests of mean abundances are achievable through collection of a relatively low number of samples. For example, the power analysis estimated that n = 22 samples were necessary to detect a 25% difference in mean drift density with a power of greater than 0.8 (Fig. 2.6). Just n = 7 and n = 3 samples were needed to detect 50% and 100% differences in mean drift density with a statistical power greater than 0.8. Fewer samples were needed to detect similar deviations in mean total drift biomass (Fig. 2.6). For example, 25% differences in mean total drift biomass could be detected with a high level of statistical power (> 0.8) with n = 14 samples per site.

To detect 50% differences in mean drift biomass n = 5 samples were needed for a statistically significant t-test with the same level of power. A 100% deviation in drift abundances may seem like a large value. However, in this study alone, which was conducted within a single basin, up to four fold differences in mean drift abundances were observed among sampling reaches. It is likely that greater differences in drifting invertebrate abundances will be found as the spatial distribution of sampling is increased.

High within-reach variance contributed to the large sample size estimates that are needed to detect 25% differences in mean benthic density with a power greater than 0.8 (Fig. 2.7). However, 100% differences in mean benthic density could still be detected with a high degree of power with n = 5 samples. Similar to drift biomass, samples of benthic biomass are more precise than density at the reach scale. T-tests for detection of mean differences in benthic biomass required roughly half the samples needed to achieve the same power for benthic density (Fig. 2.7).

Transferability of samlping methods

Simple linear regression models showed that benthic abundances were positively correlated with drift abundances with respect to both density and biomass (Table 2.4; Fig. 2.8). Samples of benthic and drift biomass featured a stronger linear correlation with one another ($R^2 = 0.51$, $p = 0.01$) than samples of benthic and drift density ($R^2 = 0.15$, $p = 0.09$).

Discussion

This study was able to demonstrate patterns in macroinvertebrate community abundances at multiple scales. Spatially, this study showed a pattern of greater variation occurring among streams, and a relatively homogeneous distribution of invertebrate abundances among stream segments on a single stream. The results reported in this study are not able to provide mechanistic linkages between observed invertebrate distributions and variation in environmental characteristics. However, these results provide a number of valuable insights concerning the structure of invertebrate communities, while also providing information that can be used to guide the design of robust invertebrate sampling protocols.

Spatial variation

Of the spatial scales considered in this study, invertebrate community abundances exhibited the greatest variation among distinct streams. This pattern was especially apparent for samples of total invertebrate drift biomass and density. Variation in samples of total drift abundance between reaches within a single stream was generally low. Similarly, within-reach variation (i.e. variation between riffles) was also less pronounced than variation in drift abundances between streams. These observations are consistent with previous studies that have evaluated spatial variation in invertebrate drift samples. For example, Matthaei et al. (1998) found that variation in drift density between reaches on a single stream was lower than the variation associated with samples

collected within a single reach. A similar study of invertebrate drift conducted on a single stream found that the variation between two stream segments separated by 800 m was of a similar magnitude to within segment variability (Shearer et al. 2002). Studies that have evaluated spatial variation in benthic density have shown that variation among streams is greater than variation within streams (Li et al. 2001).

In contrast to drift samples, the distribution of variance with respect to measurements of total benthic density versus biomass differed dramatically. Within-reach variation was far greater than variation among streams and among stream reaches for benthic density. These results are not uncommon, as previous studies have demonstrated a high degree of within-reach variation relative to among-reach variation for benthic density (Boyero 2003; Heino et al. 2004). However, the distribution of variance for measures of total biomass of benthic invertebrates was largest among streams (Table 2.2, Fig. 2.5). Variation in total benthic biomass between reaches on the same stream was also large, accounting for 24% of the total sampling variance.

These observations would suggest that in the systems evaluated in this study, invertebrate abundances are responding to environmental variation at the stream or catchment scale, and less so to local environmental differences among stream segments. Whole catchment flow regimes, associated disturbance patterns, and hydrologic characteristics affect the distribution and structure of stream macroinvertebate communities (Allan 1995). These characteristics are likely to be more related among stream segments within a single catchment.

Catchment geology also places geomorphic constraints on the distribution of meso and micro-scale habitats that determine the distribution of stream invertebrate communities at larger spatial scales (Minshall and Robinson 1998). In addition, a stream's geological setting contributes to nutrient availability, which affects primary and ultimately secondary production of invertebrate communities (Krueger and Waters 1983). Current and historic land-use patterns also differed at the stream rather than reach scale among the streams evaluated in this study. Differences in the types and extent of riparian vegetation cover found within the study area were also more pronounced among entire streams rather than reaches.

The finding of this study also demonstrated that drift abundances vary transversely across the stream channel, as depicted by the considerable variation observed between replicate drift nets (Fig. 2.3). Whether entry into the drift is intentional or unintentional, many groups of lotic invertebrate taxa are designed for clinging to the stream substrate rather than to swim in the water column (Rader 1997; Poff et al. 2006). Thus, one would expect the distribution of invertebrates entrained in the drift would be subject to flow variation occurring at the scale of a single cross-section. The presence of woody debris and channel sinuosity produce a high degree of habitat and flow complexity among the small tributary streams that were evaluated during this study. These channel characteristics likely contributed to the variation in drifting invertebrate abundances that were observed at the scale of channel cross-sections.

Studies of salmonid habitat suggest that this variation may be important from a fish perspective. Salmonids are thought to select for habitat based on how microhabitat variation in prey density and current speed interact to determine capture success rate (Hughes and Dill 1990; Hill and Grossman 1993). However, many research and monitoring activities focus on the relationship between salmonid populations and habitat attributes at the reach scale. Previous studies have shown that salmonid performance indices often track variation in resource availability at the spatial scale of streams or stream reaches (Nislow et al. 1998). Thus, any reduction of *within reach* (e.g. channel cross-section) variance will improve the ability to detect differences in drift abundance at the reach scale. Subsequent analysis of variation in invertebrate drift used pooled replicate drift nets as a single composite sample. Pooling drift nets in this manner decreased within reach variability and increased signal-to-noise ratios for samples of both total drift density and biomass. These results suggest that drift sampling precision can be increased at larger spatial scales (stream, stream reach) by utilizing a maximum amount of replicate drift nets at each sampling event, and pooling the material collected as a single sample. A similar approach would be to sample drift using drift nets with large mouth openings that are capable of sampling a maximum percentage of the total stream discharge whenever possible. Composite drift samples can be sub-sampled to circumvent increased laboratory processing times that may result from sampling greater volumes of flow.

Temporal variation

Sampling three distinct reaches at several hour intervals over a 24 h period allowed a finer description of the variation in drift abundances that occurs during the course of a single day. Among these three sampling reaches, drift abundances followed a similar diel pattern exhibiting low drift abundances during daylight hours and increased drift abundances at night. This diel periodicity of invertebrate drift has been well studied (Muller 1974), and it is thought that this pattern is a behavioral adaption used by invertebrates to avoid predation by sight feeding fishes (Flecker 1992). Studies have suggested that peak foraging by salmonids occurs at crepuscular periods when invertebrate drift rates are elevated, and salmonids can still locate prey effectively (Elliott 1973). Based on these observations, researchers have recommended that studies wishing to quantify drift abundances collect short duration samples at crepuscular periods when drift densities are at a maximum (Allan and Russek 1985). The findings of this study suggest that researchers should use caution when considering this approach. Observations from this study demonstrated up to ten fold changes in drift biomass at a single sampling location over a several hour period around dusk (Fig. 2.2). Similar fluctuations in measurements of drift density were also observed. These dramatic fluctuations observed over periods of just several hours mean that estimates of drift abundance from sampling at crepuscular periods may be highly dependent on the timing and duration of drift net deployment. To alleviate this source of within-reach variance, researchers should consider collecting drift samples over an entire 24 h period. The potential

for decreased within-reach variance offered by sampling drift over long durations is further supported by studies that have shown an increase in drift sampling precision with the duration of drift net deployment (Culp et al. 1994). Further, sampling over a short period at dusk may provide only a snapshot of the types and abundances of invertebrate drift that salmonids may be exposed to. In contrast, samples collected over an entire 24 h period may provide a more temporally aggregated description of the food resources available to salmonids throughout the course of a typical day.

In contrast to the extreme diel variation observed in drifting invertebrate abundances, variation between days at a single sampling location was low. These findings suggest that aside from diurnal periodicity, the mechanisms causing invertebrates to drift may be manifesting at temporal scales greater than a day. Invertebrates are known to enter the drift intentionally as a means of dispersal, or during emergence as adults (Brittain and Eikeland 1988). Dispersal via the drift is thought to occur as a means to seek out new habitats that feature greater resource abundances (Muller 1974). It is likely that the pressure to seek out new habitat occurs gradually, as invertebrates develop and reproduce, making resources become scarce. Similarly, large emergences of adult aquatic larvae occur as a single cohort develops, and emergences often span the course of at least several days (McCafferty 1983). Thus, the low day-to-day variation observed during this study may be characteristic for summer drift abundances.

Despite these observations, it should be noted that the samples collected in this study used to describe day-to-day variation in invertebrate drift took place

over a short period of time in mid-June when water levels and weather patterns were generally stable. These conditions likely contributed to the low amount of variance that was observed in drift abundances between days. Stream invertebrates enter the drift both intentionally and unintentionally in response to environmental conditions such as light intensity, changing weather conditions, or changes in flow (Elliot 1971). These responses may cause dramatic fluctuations in drift abundances at the temporal scale of several days.

While the results of this study suggest that day-to-day variation in invertebrate drift is low, significant temporal trends in invertebrate drift abundances across scales ranging from months to seasons have been reported in previous studies (Brittain and Eikeland 1988). In this study however drift samples collected at a single location were in agreement, regardless of whether they were collected in early or late summer. These finding are encouraging from a monitoring perspective, as it may be possible quantify drift abundances throughout a season of interest from samples collected on a single visit.

In addition to drift, monthly differences in benthic sample abundances were also evaluated during the course of this study. However, because replication in the benthic sampling design was on monthly sample dates, it is difficult to isolate the true magnitude of long term (monthly) temporal variation. No variation was detected at the temporal scale of months for total benthic density. However, results did suggest that monthly changes in benthic abundance contributed to within reach variance for total biomass. This variation

may be due to the accrual of additional body mass by aquatic invertebrates during the summer survey period.

Transferability of sampling methods

Linear regression models showed that among the stream reaches evaluated in this study, a more abundant benthic invertebrate community translated into a greater abundance of drifting invertebrates (Table 2.4, Fig. 2.9). Probably due to the increased sampling precision associated with measuring biomass, the association between benthic and drift biomass was stronger than the association between measures of benthic and drift density. The presence of this relationship suggests that a more abundant benthic community translates into increased drift, and likely an increase in the food available for drift feeding fish. This assumption has positive implications for research programs that have an interest in food availability for drift feeding fishes. Further, this relationship suggests that if a simple measure of biomass is included in routine benthic invertebrate sampling conducted by monitoring programs, inferences related to the availability of drifting invertebrates can also be made. The ability to make general predictions about drift abundances based on benthic sampling should allow comparisons to be made with other studies that collect drift instead of benthic samples.

This simple linear relationship between benthic and drifting invertebrate abundances does offer some utility. However, the propensity to enter the drift, as well as the vulnerability of lotic invertebrates as salmonid prey varies taxonomically. It is likely interpretation of benthic sample abundances as a food

resource for lotic salmonids could be refined through consideration of taxa specific life-history and behavioral traits that increase drift propensity (see Rader 1997 for an approach).

Despite the presence of a statistically significant linear relationship between drifting and benthic invertebrate abundances, the results of this study suggest that drift sampling should be used as a measure of food abundance for salmonids whenever possible. Signal-to-noise ratios for drift biomass were always greater than those of benthic biomass. Further, benthic invertebrate abundances have been shown to vary substantially at meso and micro-habitat scales, which could potentially contribute to a large amount of within reach sampling variance. It is possible that some of this within-reach variation in the distribution of benthic invertebrates is homogenized as invertebrates enter the water column to drift. This homogenization translates into greater precision for drift samples at and above the spatial scale of stream reaches.

Summary and sampling recommendations

Determining the appropriate scale at which to address a research problem remains a fundamental difficulty in ecological studies (Fahrig 1992). This is especially true for lotic salmonids, a group of species that interact with stream habitat features that exhibit variation across a wide range of spatial and temporal scales. Describing salmonid habitat processes using a multi-scaled framework will be an essential step toward the development of robust study designs that can be used to understand variation in salmonid distribution and abundance. The investigation of aquatic invertebrate abundances presented in this study has

provided a prime example of how information gained through multi-scaled research can be used during the development of such study designs. Further, this research demonstrates how the evaluation of variance, rather than mean values, can yield valuable insight about the nature of ecological processes.

Quantifying invertebrate variation provided information that can be used to adjust sampling designs and methodologies to minimize sources of sampling noise. First, regardless of whether drift or benthic samples are to be collected, a measure of biomass should always be evaluated. Measures of biomass were always more precise than measures of density whether the spatial scale of interest was at the reach or stream. Further, biomass is a more descriptive measure of food abundance as it accounts for the size as well as numbers of prey items available. As mentioned above, for studies whose primary interest in invertebrate sampling is to measure food abundances, drift samples, as opposed benthic samples should be collected. This recommendation is made not only because salmonids generally focus on invertebrates in the drift, but also because within reach sampling noise was always lower for drift rather than benthic sampling. This pattern for increased precision of invertebrate drift sampling was readily apparent in this study. Signal-to-noise ratios for samples of drift biomass among streams were as high as 7.2. Kaufmann et al. (1999) identified a set of criteria that could be used to judge the precision of indicators of stream conditions based on signal-to-noise ratios. According to this criteria, signal-to-noise ratios of 0-2 are considered to have poor precision, 2.10 is considered moderately precise, and highly precise indicators have S:N greater than 10.

This study also demonstrated how simple adjustments to sampling methodologies can be used to minimize sampling noise at finer temporal and spatial scales. One such adjustment is the recommendation that when possible, drift samples be collected over a 24 h period in order to alleviate variance due to diel periodicity. Additionally, maximizing the area of a channel cross-section sampled, and/or pooling of replicate drift net samples can be used to minimize sample variation that is due to spatial differences in drift at the scale of a stream channel cross-section.

Evaluation of invertebrate variation among the larger spatial scales of streams and stream reaches provided insight that can be used to guide development of invertebrate monitoring designs. For example, variation between reaches on a single stream was low. This was the case even among the distinct sampling reaches evaluated in this study, which were chosen because they differed substantially from one another with respect to a number of environmental features. This lack of variation between reaches suggests that large sample sizes would be needed to detect small reach scale differences in invertebrate abundances using standard statistical tests. The upshot to these findings is that large differences in invertebrate abundances that exist between streams should be easy to describe given a modest amount of sampling effort. Further, it may be possible to generalize drift or benthic sampling information across considerable distances (several kilometers in this study) based on information from samples collected at only a single location.

Perhaps the most significant result of this study is the identification of a spatial scale at which invertebrate abundances appear to exhibit the highest degree of variation. In biotic systems, it is often the scale over which variation is greatest that important interactions exist that put controls on assemblage structure. From this, it is likely that studies focusing on invertebrate abundances at the stream or reach scale have the potential to provide valuable insight about how food availability affects lotic salmonid population dynamics.

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Table 2.1. Signal-to-noise ratios for total drift density (no./100m^3) and biomass (mg/100m^3) from 2 h and 24 h samples collections calculated for separate and pooled replicate drift nets.

Sample set	Metric	Nets	S:N among streams	S:N among reaches
2 h	Drift density	separate	2.76	1.52
		pooled	3.81	2.19
	Drift biomass	separate	2.91	1.35
		pooled	4.48	2.13
24 h	Drift density	separate	2.40	1.52
		pooled	5.08	1.55
	Drift biomass	separate	2.67	1.80
		pooled	7.20	2.90

Table 2.2. Percent of total variance for benthic samples collected across streams (among stream), reaches (within stream), riffles (within reach), and months for the density (no./m^2) and biomass (mg/m^2) of major orders of aquatic invertebrate larva.

Order	Metric	Among stream	Within stream	Within reach	months
Total	density	0%	0%	36%	64%
	biomass	40%	24%	9%	27%
Coleoptera	density	0%	66%	0%	34%
	biomass	0%	65%	0%	35%
Diptera	density	53%	0%	0%	47%
	biomass	27%	0%	0%	73%
Ephemeroptera	density	0%	0%	0%	100%
	biomass	0%	4%	0%	96%
Plecoptera	density	0%	0%	0%	100%
	biomass	9%	8%	0%	83%
Trichoptera	density	0%	1%	11%	88%
	biomass	59%	25%	0%	16%

Table 2.3. Signal-to-noise ratios for benthic density (no./m^2) and biomass (mg/m^2) for the major orders of aquatic invertebrate larva.

Order	Metric	S:N among streams	S:N among reaches
Total	density	0	0
	biomass	6.38	1.35
Coleoptera	density	0.51	1.92
	biomass	0.32	1.89
Diptera	density	1.13	0.46
	biomass	0.36	0.22
Ephemeroptera	density	0	0
	biomass	0.03	0.04
Plecoptera	density	0	0.00
	biomass	0.16	0.19
Trichoptera	density	0.19	0.01
	biomass	2.86	3.92

Table 2.4. Number of observations (*n*), slope (β), intercept, coefficient of determination (R^2), and statistical significance (p) for regressions between benthic and drift sample abundances.

Metric	*n*	β (se)	Intercept (se)	R^2	p
Density	20	0.0063 (0.003)	16.49 (6.75)	0.15	0.0901
Biomass	20	0.0175 (0.004)	8.63 (6.96)	0.51	0.0106

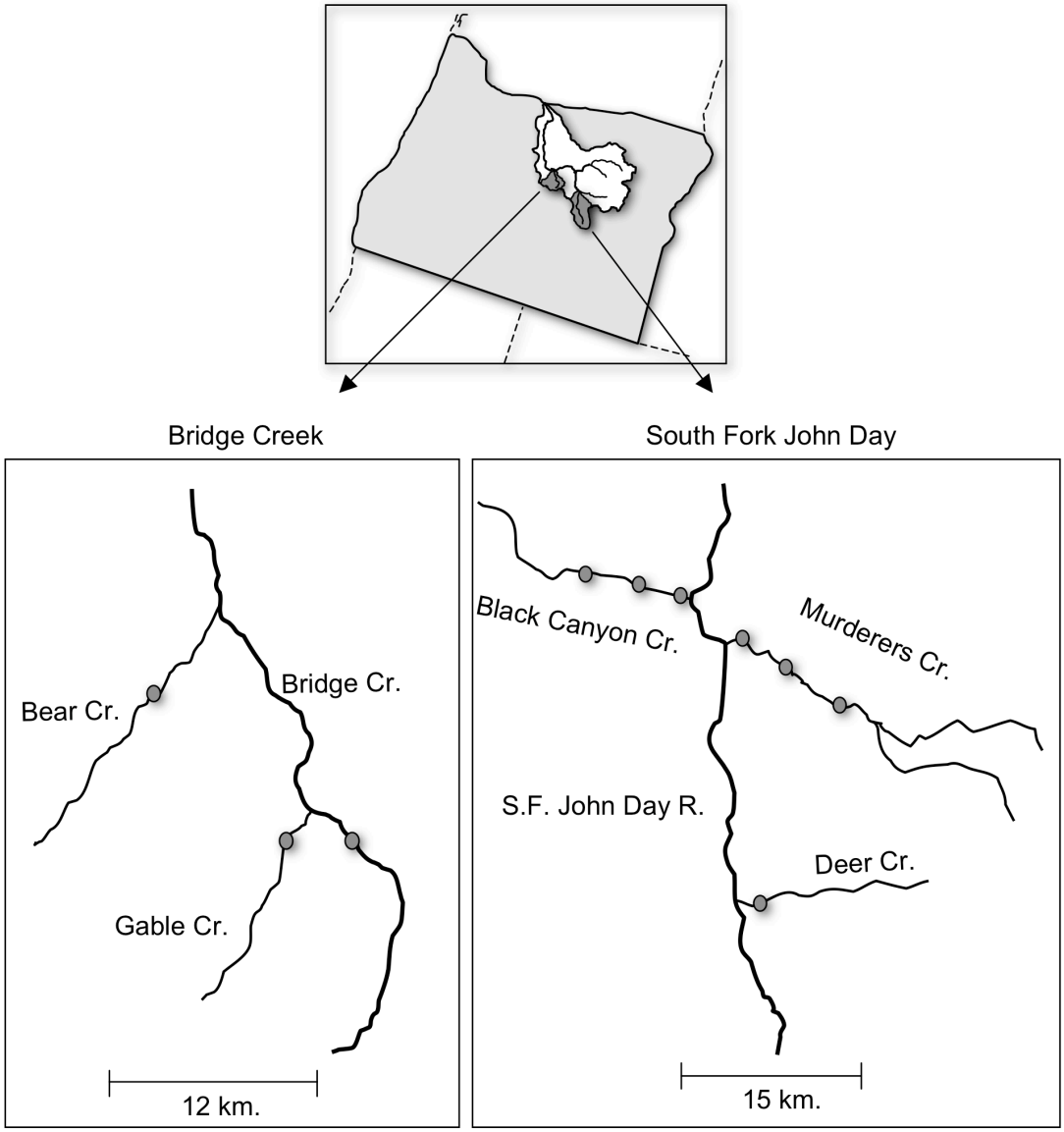

Fig. 2.1. South Fork John Day and Bridge Creek sub-basins, and approximate locations of sampling reaches (grey dots).

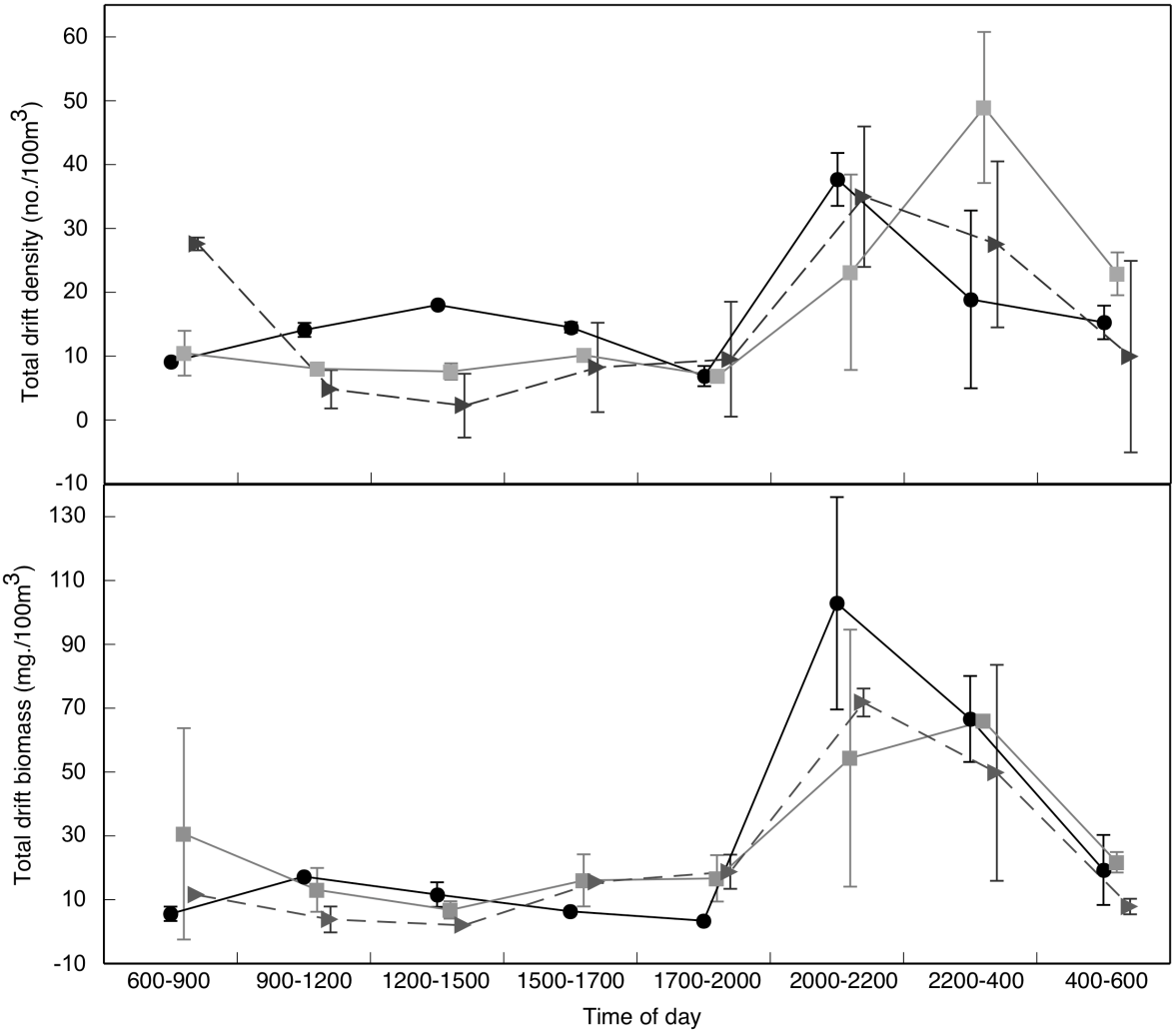

Fig. 2.2. Mean drift density and biomass recorded over a 24 h period at three study reaches. Error bars are one standard deviation.

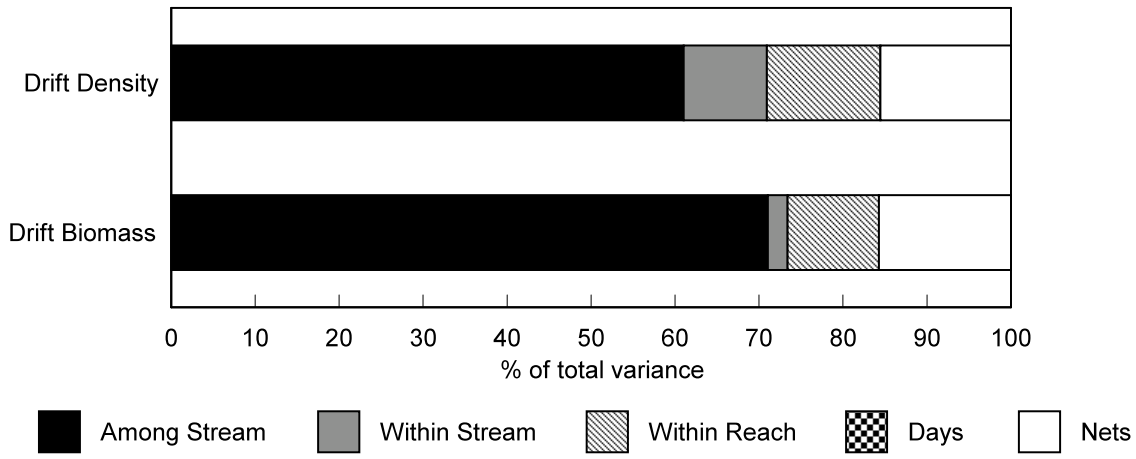

Fig. 2.3. Percent of total variance for 2 h drift samples collected across streams (among stream), reaches (within stream), riffles (within reach) and days for total drift density (no./100m^3) and biomass (mg/100m^3).

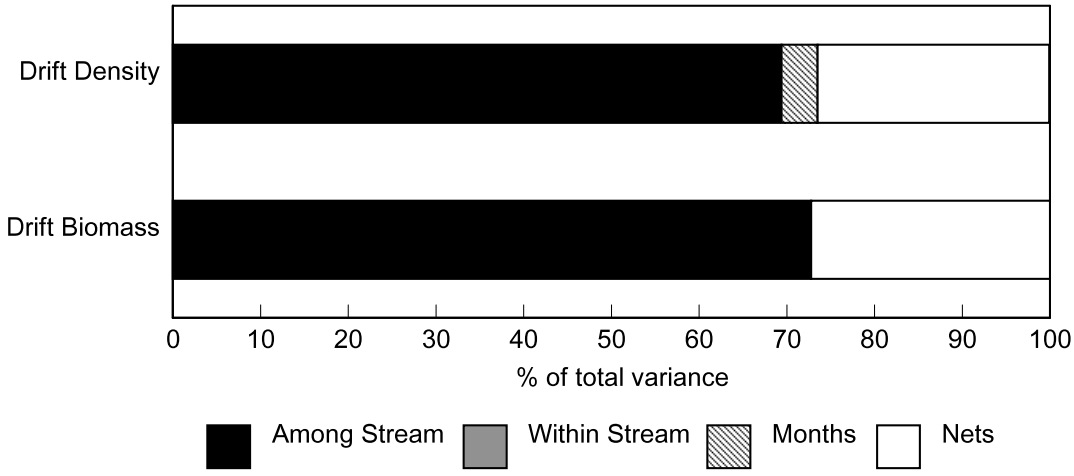

Fig. 2.4. Percent of total variance for 24 h drift samples collected across streams (among stream), reaches (within streams), and months for total drift density (no./100m^3) and biomass (mg/100m^3).

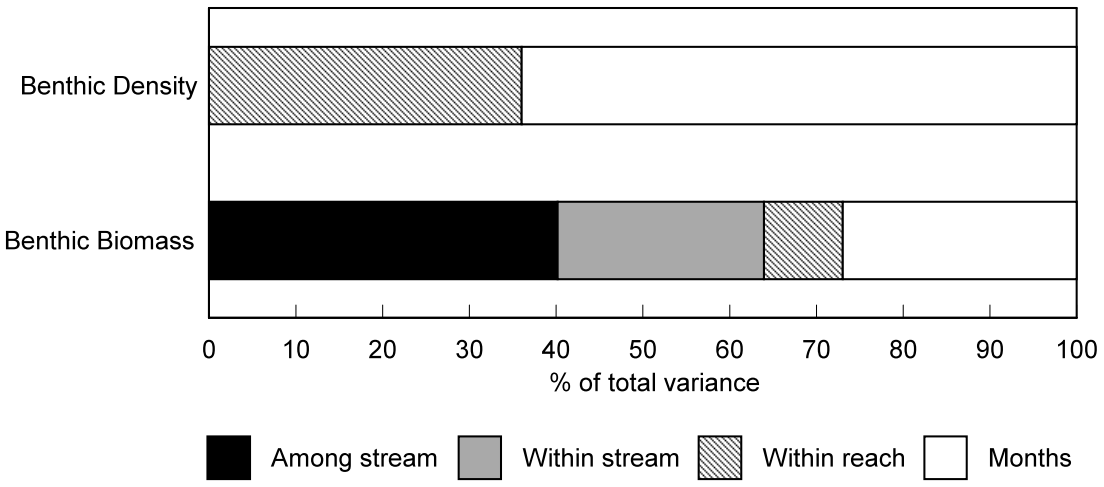

Fig. 2.5. Percent of total variance for benthic samples collected among streams, reaches (within stream), riffles (within reach), and months for total benthic density (no./m^2) and biomass (mg/m^2).

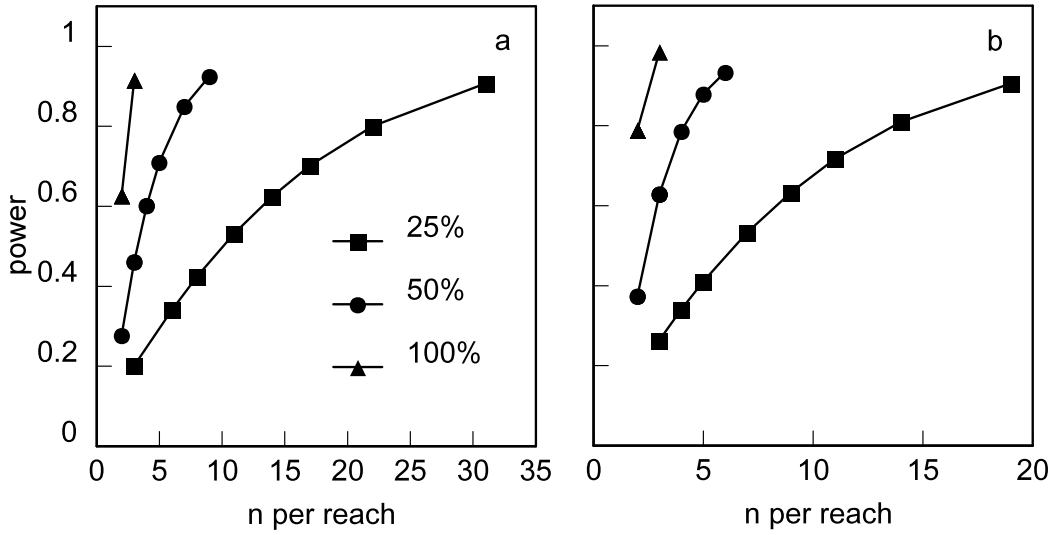

Fig. 2.6. Number of samples per reach (n) required to detect a 25%, 50%, or 100% difference in mean (a) total drift density (no./100m^3) and (b) total biomass (mg/100m^3) with associated level of statistical power.

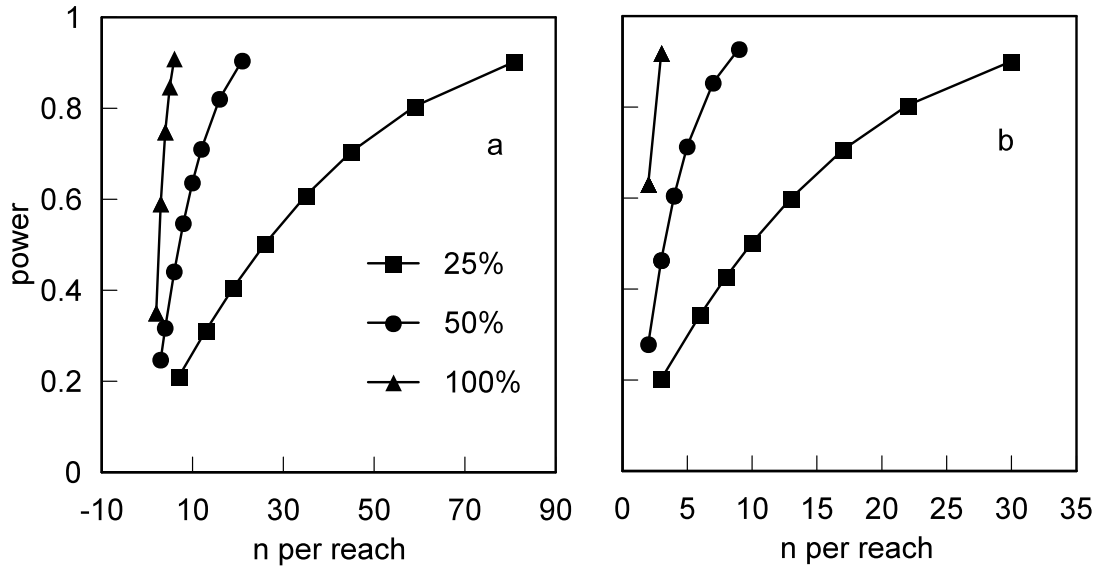

Fig. 2.7. Samples per reach (n) required to detect a 25%, 50%, or 100% difference in mean total benthic (a) density (no./m^2) and (b) biomass (mg/m^2) with associated level of statistical power.

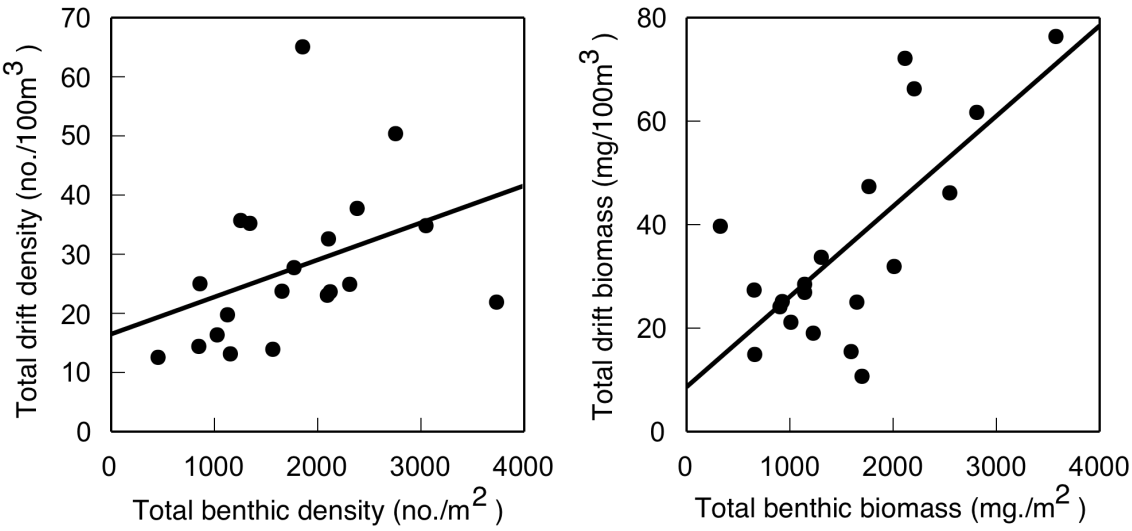

Fig. 2.8. Simple linear regressions between benthic and drift biomass and density.

CHAPTER 3

SUMMER GROWTH OF JUVENILE STEELHEAD TROUT (*ONCORHYNCHUS MYKISS GARDNERI*) IN RELATION TO FOOD ABUNDANCE AND TEMPERATURE

Abstract

Criteria used to characterize lotic salmonid habitat suitability are often based on observed correlations between physical habitat characteristics and salmonid abundances. A focus on physical habitat features ignores other habitat components, such as an adequate supply of food that set the physiological limitations on salmonid growth and survival. This study outlines the development of an approach to assessing habitat suitability that focuses on how invertebrate food availability interacts with stream temperatures to determine salmonid growth potentials. Abundances of benthic and drifting invertebrate communities, stream temperatures, and juvenile steelhead trout (*Onchorhynchus mykiss gairdneri*) summer growth rates and abundances were measured within 10 distinct stream segments in central Oregon. Stream temperatures and growth rates were used as inputs for bioenergetics model simulations to produce estimates of *O. mykiss* summer consumption rates. Measures of invertebrate abundance providing the best description of food availability were chosen based on their ability to explain observed variation in consumption. Much of the variation in *O. mykiss* consumption estimates was explained by measurements of total drift biomass

along a type II predator response curve. Jackknife validation of the best regression models predicting *O. mykiss* growth from drift biomass suggest that these models are robust, and may be applicable in additional stream systems. This study demonstrates an accessible approach for predicting salmonid habitat growth potentials based on the collection of invertebrate and temperature information.

Introduction

Many salmonid species rely on freshwater environments during various life history stages. An abundance of research conducted by ecologists and managers has been devoted to describing the interactions that exist between salmonids and freshwater habitat features. The information gained from this research is then used to assess salmonid habitat suitability, and prioritize restoration and management activities. Criteria used to assess salmonid habitat suitability are often based on observed correlations between physical habitat characteristics and salmonid density (Rosenfeld 2003). This focus on physical features in the assessment of salmonid habitat quality may stem from a fundamental disagreement among ecologists regarding the nature of limitations to the production of lotic fishes (Power et al. 1988). It has been argued that physical habitat features and the frequency and magnitude of disturbance are the primary drivers of lotic fish assemblage dynamics. In contrast, some have argued that biotic habitat components, such as an adequate supply of food, set the physiological limitations on growth and survival that ultimately determine the

production of lotic fishes (Filbert and Hawkins 1995; Rosenfeld and Boss 2001).

Both experimental and observational field studies support the hypothesis that food availability has the potential to limit stream salmonid production. For example, laboratory experiments that expose salmonids to food abundances above ambient levels report increased individual salmonid growth rates, as well as greater survival of salmonids at high population densities (Mason 1976; Boss and Richardson 2002; Rosenfeld et al. 2005). In the field, studies are often limited to the documentation of correlations between salmonid population demographics and invertebrate abundances (Cada et al. 1987; Filbert and Hawkins 1995; Johansen et al. 2005). However, food represents only a single component of stream environments and other habitat features interact with food abundance to influence salmonid growth (Boss and Richardson 2002). For this reason, correlative field studies of invertebrate abundances alone lack the ability to provide information that can be used to predict how salmonid populations may respond to variation in food availability.

For instance, the temperature regime of a stream must be accounted for when attempting to quantify the influence that food availability may have on salmonid growth. Because salmonids are ectotherms, stream temperatures dictate how consumed energy is allocated to either basal metabolic processes, or the accrual of additional tissue growth. Fortunately, the relationship between temperature and many major salmonid physiologic processes are well described (Elliott 1976; Rand et al. 1993; Rodnick et al. 2004). Because the energetic

costs (respiration, egestion, excretion) and potential gains (maximum consumption rate) are temperature dependent (Fig. 3.1), the opportunity exists to estimate salmonid growth potentials when temperature information is available. However, temperature driven models of growth operate under the assumption that fish are able to locate and consume prey at a constant proportion of their maximum physiologic rate. Tests of these models suggest that this assumption is seldom met (Railsback and Rose 1999; Dieterman et al. 2004), and that salmonid growth potential can be limited by the availability of invertebrate food resources (Cada et al. 1987; Bacon et al. 2005).

In lotic environments, salmonids primarily forage on aquatic and terrestrial macroinvertebrates (Elliott 1970; Elliott 1973; Cada et al. 1987; Romaniszyn et al. 2007). Environmental conditions at a number of spatial and temporal scales determine the composition of aquatic and terrestrial macroinvertebrate communities (Poff and Huryn 1998). From this, one would expect the types and abundances of prey available to lotic salmonids to differ among stream environments. This differential availability of prey leads to habitats that may be more or less energetically favorable, and offers the potential for food to limit individual salmonid growth.

This study focuses on the development of a framework for describing how variation in invertebrate abundances and stream temperatures interact to determine the growth rates of juvenile steelhead (*Ocorhynchus mykiss gairdneri*). This study was designed to meet two objectives. First, this study sought to quantify the contribution that invertebrate food abundances have on the growth

rates of local salmonid populations that vary with respect to their size structure and the temperature regimes they inhabit. The second objective of this study focused on identifying invertebrate sampling methodologies and measures of macroinvertebrate abundances that provide the best description of food availability for salmonids. Ideally, the information gleaned from this study will demonstrate the linkages that exist between invertebrate and fish populations, and aid in the development of simple monitoring approaches that can be used by researchers and managers to determine the degree that salmonid populations are limited by food availability.

Study area and methods

Study area

This study was conducted in several high-desert streams of central Oregon's John Day River Basin (Fig. 3.2). These streams provide important spawning and rearing habitat for wild populations of both anadromous and resident steelhead trout (*Oncorhynchus mykiss gairdneri*, hereafter *O. mykiss*). Study reaches were distributed across six streams chosen to encompass a range of temperature profiles and habitat conditions. Three study reaches were established on each of Murderers and Black Canyon Creeks, tributaries of the South Fork of the John Day River. The boundaries of these reaches were separated by roughly 2 km in stream distance. A single study reach was also established on Deer Creek, also a South Fork of the John Day tributary. Three additional study reaches were selected in the nearby Bridge Creek sub-basin of

the John Day River. A single study reach was selected on each of Bridge Creek, Bear Creek, and Gable Creek (Fig. 3.2). Study reaches ranged between 99 m and 1363 m in distance measured along the thalweg (Table 3.1).

Stream temperature

Hourly stream temperatures were recorded at each of the 10 survey reaches using temperature loggers anchored to the stream bottom. Average daily temperatures were calculated at each reach during the survey period, and used as an input for bioenergetic model simulations of *O. mykiss* growth and consumption (see below).

Macroinvertebrate sampling

An extensive set of benthic and drifting macroinvertebrate samples was used to compare the abundance and composition of macroinvertebrate communities among sites. Each drift sample collection consisted of anchoring two nets along a cross section of the stream channel with the net mouth oriented perpendicular to stream flow. The top of the net mouth was always protruding above the surface of the water to capture terrestrial and emerging aquatic invertebrates, and the bottom was suspended roughly 2 cm above the channel substrate to prevent invertebrates from crawling into the net. Drift nets had mouth openings 40 cm in height and 15 cm in width, and were composed of 1 mm Nitex® mesh. The total volume of flow sampled was estimated by multiplying the average of velocity measurements (recorded at the center of the net mouth just after setting and just before removing each net) by the total time a

net was deployed by the area of the net mouth submerged. Drift samples were collected at each site during mid-July, a time period roughly corresponding to the middle of the survey of *O. mykiss* summer growth. Sample durations spanned an entire 24 h period.

Quantitative benthic macroinvertebrate samples were collected using a 500μm Nitex® mesh surber-net that samples a fixed area of 0.09 m^2. Each benthic sample was collected by disturbing the substrate enclosed by the surber-net in eight randomly selected fast-water (riffle) habitat locations. Benthic samples were collected at each site on two dates near the middle of the summer survey period.

Both drift and benthic samples were preserved in 70% ethanol in the field prior to being transported to the lab for processing. Aquatic macroinvertebrate larvae in drift and benthic samples were identified to the level of family (Merritt and Cummins 1984). Terrestrial and emergent adult stages of aquatic invertebrates were identified to order only. Dry-weight (mg) was measured according to taxa, life-history stage, and terrestrial or aquatic origin. Aquatic larvae were grouped according to five major orders; Coleoptera, Diptera, Ephemeroptera, Plecoptera, and Trichoptera. Aquatic larvae not belonging to these orders were weighed separately and generally accounted for a small percentage of the total sample dry-weight. Drift samples were partitioned into two additional groups consisting of adult life stages of aquatic invertebrates and terrestrial invertebrates. The weight of each group partition was recorded after being placed in a drying oven at 60^{O}C for a minimum of 24 h, or until samples

had reached a constant weight. Dry-weight of each sample partition was measured to the nearest 1 mg. The dry weights were adjusted for losses due to preservation in ethanol using conversions from our own unpublished data.

The density (count) and biomass of drifting invertebrates per volume of water sampled was calculated for each sampling date during the entire 24 h sampling period. These estimates were calculated by dividing the pooled count or dry-weight for each invertebrate group retained in the two replicate drift nets by the total volume of water sampled by both nets. Benthic invertebrate abundances were calculated for each sampling date by dividing the count or dry-weight of each invertebrate group by the total area sampled.

O. mykiss growth and density

Ocorhynchus mykiss were tagged with Passive Integrated Transponder tags (PIT-tags) in order to obtain measures of individual *O. mykiss* growth rates in each study reach. Active capture and tagging of *O. mykiss* was conducted at each reach over two consecutive days at the start of the survey in early summer and again at the end of the survey in the fall (Table 3.1). Capture methods consisted of herding *O. mykiss* into a bag seine by snorkeling or electrofishing at low output. These methods are thought to minimize the disturbance to salmonids during capture. Upon capture, *O. mykiss* were anesthetized, weighed to the nearest 0.1 g, and scanned with a handheld PIT-tag reader to determine whether a fish had been previously captured. At first capture, *O. mykiss* were tagged with a PIT-tag and the PIT-tag code was recorded. The PIT-tag code of recaptured *O. mykiss* was also recorded. Following recovery from anesthetic, *O. mykiss*

were released back to their approximate capture location within the reach.

The use of PIT-tags enabled us to identify individual *O. mykiss* that were captured in the same reach during both the early summer and fall sampling events. This allowed calculation of individual *O. mykiss* growth as the change in weight during the study period. Growth rates for each fish were summarized as the percent change in body weight per day (%/day) by dividing the change in weight, by weight at first capture, divided by the total number of days between captures, multiplied by 100.

PIT-tagging over two consecutive days also allowed us to obtain a mark-recapture population estimate of the number of *O. mykiss* occupying each survey reach. Population estimates of age 1+ *O. mykiss* were obtained from the June sampling event using the Chapman equation (Seber 1982). Because each stream was approximately the same width, density of *O. mykiss* (no./m) in each reach was calculated by dividing population estimates by reach length.

Bioenergetics modeling

Bioenergetics model simulations were used to account for the influence that variation in consumption, stream temperatures, and fish size has on *O. mykiss* growth. The bioenergetics model was configured for *O. mykiss* (Hanson et al. 1997), and incorporated updated parameter values for respiration and consumption (Railsback and Rose 1999). Each simulation was run on a one-day time step using average daily temperature values. Each model run used a constant predator energy density of 5900 J/g wet-weight (Van Winkle et al. 1998), invertebrate prey energy densities were set at 2500 J/g wet-weight.

Evaluation of stomach contents indicated that *O. mykiss* within the study area consumed a diet composed entirely of aquatic and terrestrial invertebrates.

Food limitations

Bioenergetics model simulations were used to isolate the contribution that consumption had on observed growth for *O. mykiss* occupying each of the distinct temperature regimes encompassed within the study area. To do this, the model is used to estimate daily consumption values so that growth predicted by the model matches observed growth during the survey period. Consumption is estimated based on the value of the parameter P (P-value), which describes the fraction of maximum consumption rate at which a fish occupying a given temperature had to feed in order to achieve an observed change in weight. Because P-values are a fraction between 0 and 1, they provide a standardized measure of fish consumption that is comparable among fish of unequal sizes occupying stream environments that vary with respect to temperature. In essence, P-values provide a proximate measure of how well a fish is able to meet or exceed its metabolic requirements, and should be related to environmental factors such as food availability that affect consumption (Hansen et al. 1993). It was hypothesized that if food abundance was limiting *O. mykiss* growth, one or more of the measures of invertebrate abundance would explain the observed variation in estimated P-values. This hypothesis was tested in a series of linear and nonlinear regression models treating the measures of invertebrate food abundance described above as independent variables, and the mean of individual *O. mykiss* P-values as a response. Each linear regression

model was limited to include only a single measure of invertebrate abundance. However, because density-dependence (competition for food) has the potential to limit consumption, multiple regression models containing both a single invertebrate metric as well as *O. mykiss* density were also included in the analysis.

The above linear relationship between food abundance and *O. mykiss* consumption, in which consumption increases at a constant proportion of food abundance, has been described as a type I functional feeding response. This model of consumption is unrealistic at high food levels, because at some point animals will reach satiation, or consumption will be limited by the time it takes to handle and search for prey. For this reason, nonlinear models of predator consumption in relation to prey density were also considered in the analysis. A more realistic model of predator consumption is described by the type II predator response curve (Holling 1959; O'Brian et al. 2001). The type-II curve defines not only predator consumption (k) in response to prey density (N), but also defines a maximum rate of predator consumption (D). The type II predator response equation takes the form:

$$P = \frac{kN}{D + N}$$

where P equals P-value estimates of consumption from bioenergetics model simulations. *Oncorhynchus mykiss* density was not considered in nonlinear regression models due to the large number of parameters that would need to be estimated from the sparse dataset which contained only 10 observations.

The ability of each measure of invertebrate abundance and *O. mykiss* density to explain variation in *O. mykiss* P-values in linear and nonlinear models was compared through evaluation of adjusted coefficient of determination (adj. R^2) and the direction and significance of parameter values. Observations from Bear Creek (BR) were dropped from the analysis because it went nearly dry during the survey period, forcing fish into isolated pools and making accurate quantification of drift difficult.

Model validation and application

The flexibility of the bioenergetics model was further utilized in a series of simulations intended to validate the best regression models of *O. mykiss* consumption. These simulations also served to demonstrate the ability to improve the accuracy of bioenergetic estimates of salmonid growth that rely solely on temperature information through consideration of food abundance. Yet another additional set of bioenergetics model simulations was also conducted to explore the spatial scale at which this approach could be used to make predictions of salmonid consumption.

Lacking an external dataset, a data resampling technique commonly referred to as jackknifing was used to validate the best models predicting *O. mykiss* consumption (Dixon 1993). Jackknifing is a process of removing a single observation from a dataset, and refitting a model to estimate new parameters based on the reduced dataset. Regression parameter estimates from the reduced dataset were then used to estimate a new response (P-value) for the observation that had been removed. This process was repeated until the entire

dataset had been resampled. The jackknifing procedure was conducted for both the best linear and nonlinear regression models predicting *O. mykiss* consumption. Jackknifed P-values estimated from the resampling procedure were then fed into bioenergetics model simulations in order to produce new growth estimates for each fish in the survey. The validity of each model was assessed by regressing the mean of growth predicted from jackknifed linear (G_L) and nonlinear (G_N) models to the mean of observed growth (G_O) for each site. Regressions containing the more robust model of consumption would be expected to feature a slope near 1, an intercept near 0, a high coefficient of determination (R^2), and low root mean square for error (RMSE).

Next, an additional set of bioenergetics simulations were run that were designed to demonstrate how invertebrate information can be used to increase the precision of bioenergetic estimates of growth based only on temperature. To do this, the bioenergetics model was used to produce new estimates of growth for each fish in the dataset using site specific temperatures, while holding consumption at a constant proportion of maximum consumption. To hold consumption constant, the parameter P was set to a fixed value of 0.35, the average observed P-value for fish in the study. The precision of the temperature model was assessed by comparing the agreement between the mean *O. mykiss* growth for each site predicted when consumption is held constant (G_T) to observed average growth (G_O) using linear regression.

Lastly, a final set of bioenergetics simulations were used to explore the spatial extent over which invertebrate information could be used to estimate

salmonid consumption and growth. In two of the six study streams (Murderers and Black Canyon Creeks), invertebrate abundances were measured at the spatial scale of reaches (i.e. stream segments separated by 1 to 2 km). Previous research suggests that variation in both drifting and benthic community abundances may be most pronounced between streams, and less so between reach segments within streams (see Chapter 2). Based on this observation, these model simulations were designed to test how accurately observed *O. mykiss* growth could be estimated at the reach scale using invertebrate information collected at the spatial scale of streams. This scenario was evaluated by averaging invertebrate sample abundances across survey reaches on the same stream, and incorporating these values into the best regression models predicting *O. mykiss* consumption to estimate stream specific P-values. These P-values were then incorporated into bioenergetics model simulations with reach specific temperature information to produce new estimates of growth for each fish in the survey. The drop in precision associated with generalizing invertebrate information to the spatial scale of streams was assessed in a linear regression model of average growth at the stream scale (G_S) to observed average growth at the reach scale (G_O).

Results

Stream temperatures

The survey reaches considered in this study encompassed a broad range of summer temperature regimes. The average of summer stream temperatures

was 12.35^{o}C at the coolest site (BC3) and 19.48^{o}C at the warmest site (MC1). Maximum average daily temperatures reached almost 25^{o}C on MC1, a temperature that is well above the thermal optima for *O. mykiss* (Fig. 3.1). In contrast, at the coolest site, BC3, average daily temperatures were below 15^{o}C during the duration of the summer survey (Fig. 3.3).

Macroinvertebrate abundances

Large differences in the abundance of drifting and benthic invertebrate assemblages were observed among the survey reaches. Mid-summer total drift biomass differed by over four fold among reaches, occupying a range from 15 to as high as 70 mg/100m^3 (Fig. 3.4). Mid-summer total drift density also exhibited considerable variation among survey reaches, ranging from roughly 17 to 70 no./100 m^3. Variation in total benthic abundances among survey reaches was also large, with values ranging between 760 to 3175 mg/m^2 and 1050 to 3040 no./m^2 for total benthic biomass and density, respectively (Fig. 3.5).

O. mykiss growth and density

O. mykiss summer growth rates differed by an order of magnitude among survey reaches. On Bear Creek (BR) growth was as low as 0.02 %/day. In Bridge Creek (OD), the average growth rate was 0.5 %/day (Table 3.3, Fig. 3.6). *O. mykiss* population densities occupied a large range among the survey reaches from 0.089 to 1.74 no./m (Table 3.3). The average of estimated P-values among reaches ranged between 0.30 and 0.41.

Food limitations

A multiple linear regression model featuring *O. mykiss* density and total drift biomass explained the greatest amount of variation in mean *O. mykiss* consumption (P-values) (Table 3.4). In this model, mean consumption decreased in relation to *O. mykiss* density, and increased in relation to total drift biomass (Table 3.5). Total drift biomass also explained the greatest amount of variation in *O. mykiss* consumption in nonlinear type II functional response models (Table 3.4, Table 3.6, Fig. 3.7).

Model validation and application

Results of the internal validation procedure indicated that both the best linear and nonlinear models explaining *O. mykiss* consumption were robust (Table 3.7, Fig. 3.8). Jackknifing of the best linear model (*O. mykiss* density and total drift biomass) yielded mean growth rate estimates (G_L) that explained much of the variation in observed *O. mykiss* growth rates in linear regression models. Mean growth estimates produced by jackknifing the best nonlinear type II predator response model (G_N) explained slightly more of the variation in observed mean growth than that of the best linear model. The slopes of the linear regression between G_O and G_N was closer to a value of 1 than the regression of G_O and G_L. The slopes of each of these regressions were statistically significantly different than zero ($p < 0.05$).

Linear regression models of growth estimated by bioenergetics simulations in which consumption was held constant (G_T) explained little of the variation in observed mean growth (Table 3.7, Fig. 3.8). The slope of this

regression line deviated substantially from 1, and was not statistically significant. Growth estimates produced using invertebrate abundances averaged across reaches within streams also did a poor job in reproducing observed mean growth rates (Table 3.7, Fig. 3.8).

Discussion

The results of this study demonstrated a strong positive correlation between measurements of invertebrate abundance and estimates of *O. mykiss* consumption. These results suggest that salmonids were able to increase their consumption in relation to invertebrate abundances, and that food availability has the potential to limit the summer growth rates of lotic salmonids. Statistical validation techniques suggested that fitted regression models predicting *O. mykiss* consumption from measurements of invertebrate abundances offer a level of generality that may make them applicable in additional stream systems outside this study area. Further, this study demonstrated that temperature alone (i.e. reach specific temperature with consumption held constant) did a poor job predicting observed summer growth rates of *O. mykiss*, and that consideration of how food availability may affect consumption can improve the accuracy of bioenergetic predictions of salmonid growth rates.

Measures of food availability

The dynamic nature and spatial heterogeneity of lotic macroinvertebrate communities, coupled with variation in salmonid foraging habits makes relating food resource abundance to salmonid consumption and growth a difficult task. It

is generally accepted that lotic salmonids primarily feed on aquatic and terrestrial invertebrates entrained in the water column (Elliott 1973). Thus, invertebrate drift samples should be representative of food availability. However, diurnal variation associated with invertebrate drift abundances (Muller 1974) creates uncertainties concerning when drift samples should be collected if the aim of sampling is to describe salmonid food availability. Drift abundance is thought to be greatest during low-light periods and generally low during mid-day. Thus, drift samples collected at different periods within a single day have the potential to produce different estimates of drift abundance. This is especially true when attempting to sample around crepuscular periods. Because salmonids are visual predators, it is likely that they forage during daylight hours when drift abundance may be low, but prey detectability may be high. However, it has also been suggested that peak salmonid foraging may occur during crepuscular periods when drift abundances may be at a maximum (Waters 1962; Elliott 1973). Sampling drift abundances over an entire 24 h period alleviates many of these sources of uncertainty. Because samples are collected over an entire 24 h period, sampling should not be subject to variation caused by diel periodicity. Also, sampling for an entire 24 h period may provide a more aggregated picture of the level of food abundances that salmonids experience throughout the course of a day.

In stream environments that have adequate flow, foraging directly on invertebrate drift is likely the most energetically favorable feeding strategy for lotic salmonids (Hughes 1998). However, salmonids are plastic in their foraging

habits, and epibenthic foraging has also been observed, especially during periods of low flow or low drift abundance (Tippets and Moyle 1978; Angradi and Griffith 1990; Nakano et al. 1999). However, it is likely that the vulnerability of invertebrates occupying the stream substrate varies with respect to taxa and life-stage (Rader 1997). Thus, a scheme that classifies invertebrates based on their vulnerability may be necessary before benthic (surber) sample abundances can be interpreted as food for salmonids (see Rader 1997). Further, benthic (surber) samples do not sample allochthonous inputs of terrestrial invertebrates which are a potentially important source of forage for stream salmonids (Cada et al. 1987; Huryn 1996; Wipfli 1997; Allan et al. 2003).

The results of this study corroborate these observations concerning predator-prey relationships of stream salmonids and stream macroinvertebrates. Save for a single observation that was removed from the analysis (Bear Creek), all of the stream survey reaches evaluated in this study had summer discharges and velocities that would be considered adequate for stream salmonids to forage effectively from the drift (Railsback and Harvey 2002). Total drift biomass collected over a 24 h period explained the largest amount of observed variation in *O. mykiss* consumption using both multiple linear regression and nonlinear regression models. Much of the total biomass and density (count) of drift samples were composed of terrestrial insects that had accidently been entrained in the drift, suggesting that terrestrial inputs contributed to the amount of prey available during summer for the salmonids populations in this study area (Fig. 3.4). Benthic sample abundances explained less of the variation in *O. mykiss*

consumption. However, the results of this study did demonstrate positive linear and nonlinear correlations between *O. mykiss* consumption and the benthic abundances of diptera, ephemeroptera, and trichoptera (Table 3.4, Table 3.5). These taxonomic groups are thought to have a high propensity to drift, and are thus suspected to be more vulnerable to salmonids than other benthic invertebrate taxa (Rader 1997).

Models explaining O. mykiss consumption

The agreement between the best linear and nonlinear regression models indicated that salmonids the salmonid populations evaluated in this study were able to increase their consumption rate in locations featuring greater abundances of invertebrate drift. The best multiple linear regression model predicted *O. mykiss* consumption as a function of total drift biomass and *O. mykiss* population density (fish/m). The negative value of the linear association between consumption and fish density suggests that density-dependent competition may limit salmonid food acquisition (Table 3.5). From these results alone it is difficult to place a mechanism on the nature of this competitive interaction, as competition may be occurring directly for limited food resources or indirectly for the space in which to forage effectively (Chapman 1966; Keeley and Grant 1995; Keeley 2003; Imre et al. 2004).

The best nonlinear regression model explained less of the observed variation in *O. mykiss* consumption than the best multiple regression model (Table 3.4). However, this model may offer a more plausible description of the relationship between summer food abundances and *O. mykiss* consumption.

From a statistical standpoint, this model relies on fewer parameters, and offers a more parsimonious explanation of the observed data (Johnson and Omland 2004). The type II predator response curve also places a ceiling on predator consumption rates, and offers a more realistic description of predator consumption dynamics. Further, type II predator response curves have successfully predicted salmonid consumption in relation to prey abundance in previous studies (Budy 1996; O'Brian et al. 2001; Guensch et al. 2005). The type II model also performed better than the best multiple linear regression model of consumption in the jackknife validation trials.

Interestingly, when fitting the type II predator response curve to bioenergetic P-value estimates, the asymptote for maximum consumption was predicted to occur at a P-value of less than 0.50. This raises the question of why the regression model would predict a maximum consumption rate (P-value) to occur at only 50 percent of the maximum consumption rate used in the Wisconsin bioenergetics model (Hanson et al. 1997)? One can speculate that this phenomenon is in part due to the methods used in the estimation of the bioenergetics parameters for maximum consumption. Bioenergetics model parameters are estimated during laboratory trials that seek to establish physiological maximums. For this reason, calorically dense (i.e. J/g > 2500) feed is used to avoid physical satiation due to stomach volume constraints (Rand et al. 1993). Stream macroinvertebrates contain non-digestible parts and are generally much less energetically dense. This results in a decreased maximum consumption rate that is limited by way of stomach fullness as opposed to the

physiological processes of absorption and digestion. The relatively low range of P-values observed in this study are not uncommon, as field studies of salmonid growth rates in which the Wisconsin bioenergetics model has been applied report P-value estimates that rarely exceed 0.4 (Railsback and Rose 1999; Dieterman et al. 2004) The maximum P-value observed in this study had a value of 0.51. From this, it is safe to assume that the P-value predictions made by the type II predator response model are reasonable for stream salmonids.

Noting that estimated consumption appears to reach a maximum highlights the low range occupied by the P-value parameter. The average estimated P-values among *O .mykiss* populations at each reach ranged between only 0.30 and 0.41 (Fig. 3.6). However, the bioenergetics model is extremely sensitive to the value of the parameter P, and small deviation have the potential to produce several fold differences in estimates of salmonid growth rates over short time periods (Railsback and Rose 1999). This study provides an example of the sensitivity of the bioenergetics model to the value of the parameter P, as the observed P-values for fish populations at each reach were estimated based on growth rates that differed by up to an order of magnitude (Fig. 3.6).

An additional set of bioenergetics model simulations was used to further demonstrate the impact that the range of P-values observed in this study may have on estimates of salmonid growth. To demonstrate this, a series of bioenergetics models were run using the temperature regime from the warmest (MC1) and coolest (BC3) reaches. Under each temperature regime, the growth of a 25 g *O. mykiss* was estimated using the highest (0.40) and lowest (0.30)

reach average P-value observed in this study. Under the warmest temperature regime, growth was predicted to be negative when the lower P-value was used in the bioenergetics model, and positive growth was achieved when the greater P-value was used. Under the coolest temperature regime both P-values produced positive growth. However, salmonids feeding at the higher P-value featured estimated growth rates that were almost an order of magnitude greater than growth predicted using the lower P-value. The results of this exercise clearly demonstrate the sensitivity of the bioenergetics model to small differences in the value of P, and lend further support to the importance of variation in food availability as a determinate of salmonid summer growth rates.

Estimation of salmonid habitat quality

Bioenergetics based models offer an appealing tool for estimating salmonid habitat quality because they are mechanistically linked to processes that control salmonid growth (Hansen et al. 1993). The bioenergetics models being applied to this task seem to fit one of two general descriptions. The first are relatively simple models that are driven solely by temperature. These models classify habitat suitability according to how potential metabolic costs and gains vary with respect to temperature. Temperature driven models of habitat suitability are appealing because they require only measurements of stream temperature. However, temperature driven models of growth are unrealistic because they ignore other components of habitat such as food availability that affect growth. The results of this study demonstrate the need to consider how variation in consumption can affect salmonid growth. Estimates of *O. mykiss*

growth produced by the bioenergetics model using site specific temperatures but holding consumption constant were drastically different than observed growth.

Another set of bioenergetics based models rely on high-resolution habitat information to model salmonid energetic gains and losses as a function of velocity, invertebrate abundances, physical stream habitat characteristics, and temperature (Huryn 1996; Hayes et al. 2000; Hughes et al. 2003; Guensch et al. 2005; Hayes et al. 2007). Although these models do account for habitat differences in food abundance, they are less accessible due to increased data collection and computational requirements (Rosenfeld 2003).

Requiring collection of only stream temperatures and invertebrate drift, the approach to estimating stream trout growth described in this study improves upon purely temperature driven models and is more accessible than complex bioenergetics/foraging based modeling approaches. *Oncorhynchus mykiss* growth rates predicted by resampling (jackknifing) this studies data using both the best linear (G_L) and nonlinear (G_N) models were highly related to observed growth rates (G_O). These jackknifed growth estimates, which accounted for *O. mykiss* consumption in relation to food availability, were much more accurate than growth predicted using temperature alone (Table 3.7, Fig. 3.8).

Spatial considerations for model application

The regression models predicting *O. mykiss* consumption were derived from observations of invertebrate community characteristics and salmonid growth rates collected at the spatial scale of stream segments. Fish were sampled over

reaches that ranged from roughly 200 to 700 m, and invertebrate samples were collected within these reaches. Multiple reaches sampled on the same stream (Murderers Creek and Black Canyon Creek) were separated by distances of several kilometers. If the approach to estimating salmonid consumption that is presented in this study is to be utilized, fisheries managers and researchers must give consideration to the appropriate spatial scale in which it is to be applied. For instance, how is invertebrate sampling effort to be distributed if its intended use is to make stream-wide predictions of *O. mykiss* consumption? Previous research has indicated that the largest sources of spatial variation in invertebrate drift is attributable to stream or catchment scale features. Thus, one would expect that reasonable predictions of *O. mykiss* consumption could be made over considerable stream distances through sampling of invertebrate drift in only a limited number of locations. When coupled with longitudinal temperature information, these consumption estimates could be incorporated into a bioenergetics model to make accurate predictions of *O. mykiss* growth potential.

The results of this study also show that researchers should be cautious when extrapolating measurements of invertebrate abundance over large stream distances. Invertebrate drift and benthic sample abundances collected on the most upstream survey reach of Murderers Creek (MC3) were much lower than those collected in the middle (MC2) and downstream reach (MC1). In contrast, although the distances between survey reaches on Black Canyon Creek were similar to those of Murderers Creek, invertebrate samples on Black Canyon Creek occupied a relatively low range of values. The results of this study also

demonstrated the potential decrease in accuracy that could result when using localized invertebrate sample information to predict salmonid growth at larger spatial scales (Table 3.7, Fig. 3.8).

Summary

In summary, this study demonstrated the potential for invertebrate food abundance to limit the individual growth of juvenile *O. mykiss* in nine relatively diverse stream segments. Although the observations presented in this study are limited to summer and early fall, measures of total drift biomass collected over a 24 h period were highly related to estimates of salmonid consumption. These findings support the assumption that juvenile salmonids mainly forage on drifting invertebrates. Prior to application, the relationships between salmonid consumption, growth, and invertebrate abundances that were developed within this study should be refined and tested on novel systems. However, the jackknife validation procedures would suggest that these relationships may be robust and potentially broad in application.

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Table 3.1. Reach lengths (m), survey start and end dates, and days of growth for fish at each of the ten survey reaches.

		Reach length	Survey period duration		
Stream	Reach	m	start	end	days
Black Canyon	BC1	266	25-Jun	7-Sep	74
	BC2	261	1-Jul	11-Sep	72
	BC3	170	1-Jul	11-Sep	74
Bear Creek	BR	465	22-Jun	16-Sep	95
Deer Creek	DC	283	29-Jun	4-Sep	67
Gable Creek	GC	717	18-Jun	18-Sep	98
Murderers Creek	MC1	363	23-Jun	3-Sep	72
	MC2	391	27-Jun	9-Sep	74
	MC3	99	27-Jun	9-Sep	74
Bridge Creek	OD	1363	18-Jun	10-Oct	116

Table 3.2. Mid-summer discharge, summer average daily temperature, and the maximum average daily temperature recorded during the survey period.

		Discharge	Avg daily	Max of avg.
Stream	Reach	m^3/s	Temp. (^oC)	daily temp. (^oC)
Black Canyon	BC1	0.23	15.32	18.52
	BC2	0.21	13.97	16.85
	BC3	0.23	12.35	14.62
Bear Creek	BR	0.03	18.04	21.99
Deer Creek	DC	0.04	14.13	17.76
Gable Creek	GC	0.05	15.15	18.93
Murderers Creek	MC1	0.21	19.48	24.38
	MC2	0.13	17.67	22.17
	MC3	0.05	15.32	19.42
Bridge Creek	OD	0.5	14.49	18.92

Table 3.3. Number of fish sampled (n), average percent growth per day, average P-value for bioenergetic simulations, and fish density per linear meter for each survey reach.

Reach	n	Avg. growth g/g/d	Avg. P-value	Density (1+) no./m
BC1	35	0.1 (0.02)	0.31 (0.006)	1.654
BC2	27	0.3 (0.06)	0.33 (0.009)	1.345
BC3	17	0.36 (0.09)	0.34 (0.008)	1.014
BE	16	0.02 (0)	0.33 (0.01)	0.231
DC	42	0.42 (0.06)	0.33 (0.006)	0.301
GC	13	0.47 (0.13)	0.4 (0.01)	1.384
MC1	7	0.09 (0.03)	0.38 (0.013)	1.740
MC2	34	0.32 (0.06)	0.39 (0.007)	0.589
MC3	8	0.08 (0.03)	0.31 (0.012)	0.160
BR	13	0.5 (0.14)	0.4 (0.01)	0.089

Table 3.4. Linear and nonlinear (type II functional feeding response) regression models predicting *O. mykiss* consumption (average P-values) sorted according to adjusted R^2.

Model type	Variables in model		k	Adj. R^2
linear	*O. mykiss* density	drift total biomass	3	0.89
	O. mykiss density	drift trichoptera biomass	3	0.88
	O. mykiss density	benthic ephemeroptera biomass	3	0.85
	O. mykiss density	benthic trichoptera biomass	3	0.84
	O. mykiss density	drift terrestrial biomass	3	0.84
	O. mykiss density	drift terrestrial density	3	0.83
	O .mykiss density	drift trichoptera density	3	0.82
	O. mykiss density	drift diptera biomass	3	0.82
	O. mykiss density	benthic total biomass	3	0.80
	O. mykiss density	benthic trichoptera density	3	0.80
	O. mykiss density	benthic total density	3	0.80
	O. mykiss density	benthic diptera biomass	2	0.79
	O. mykiss density		*2*	0.79
nonlinear	drift total biomass		2	0.67
	benthic diptera biomass		2	0.59
	drift adult biomass		2	0.49
	drift total density		2	0.36
	drift emergent density		2	0.34
	drift diptera biomass		2	0.34
	benthic total biomass		2	0.32
	benthic trichoptera biomass		2	0.27
	benthic trichoptera density		2	0.26
	benthic total density		2	0.23

Table 3.5. Parameters values and y-intercept for best multiple linear regression models predicting *O. mykiss* consumption (P-values).

Best linear regression models				
	β1 (se)		β2 (se)	y-int.
O. mykiss density	-0.044 (0.0082)*	drift total biomass	0.00074 (0.0003)*	0.37
O. mykiss density	-0.044 (0.0083)*	drift trich. biomass	0.0048 (0.0019)*	0.38
O. mykiss density	-0.048 (0.0092)*	benthic ephem. biomass	0.00013 (0.00007)	0.38
O. mykiss density	-0.046 (0.01)*	benthic trich. biomass	0.000015 (0.000009)	0.38
O. mykiss density	-0.05 (0.009)*	drift terr. biomass	0.0014 (0.00083)	0.39

*indicates parameters values statistically significantly different than 0 at $\alpha = 0.1$

Table 3.6. Parameter values and standard errors for type II functional feeding response of *O. mykiss* P-values and food abundance. All models were significant at $\alpha = 0.1$.

best type II functional feeding models		
Variable in model	k (se)	D (se)
drift total biomass	0.44 (0.026)	5.89 (1.8)
benthic diptera biomass	0.41 (0.02)	10.9 (3.6)
drift adult biomass	0.43 (0.03)	1.05 (0.41)
drift total density	0.44 (0.04)	4.44 (2.3)
drift adult density	0.41 (0.03)	0.8 (0.42)

Table 3.7. Slope, y-intercept, root mean square for error (RMSE), coefficient of determination (R^2), and significance of regressions of average observed growth (G_O) and average growth predicted from jackknifing the best linear (G_L) and nonlinear (type II) models (G_N), from fixed consumption (G_T), and from stream average invertebrate information (stream, G_S).

Model	Slope	y-int.	RMSE	R^2	*p*
G_L	0.93	0.04	0.027	0.5	0.03
G_N	0.9	0.02	0.019	0.57	0.02
G_T	0.22	0.19	0.026	0.05	0.55
G_S	0.56	0.14	0.018	0.35	0.09

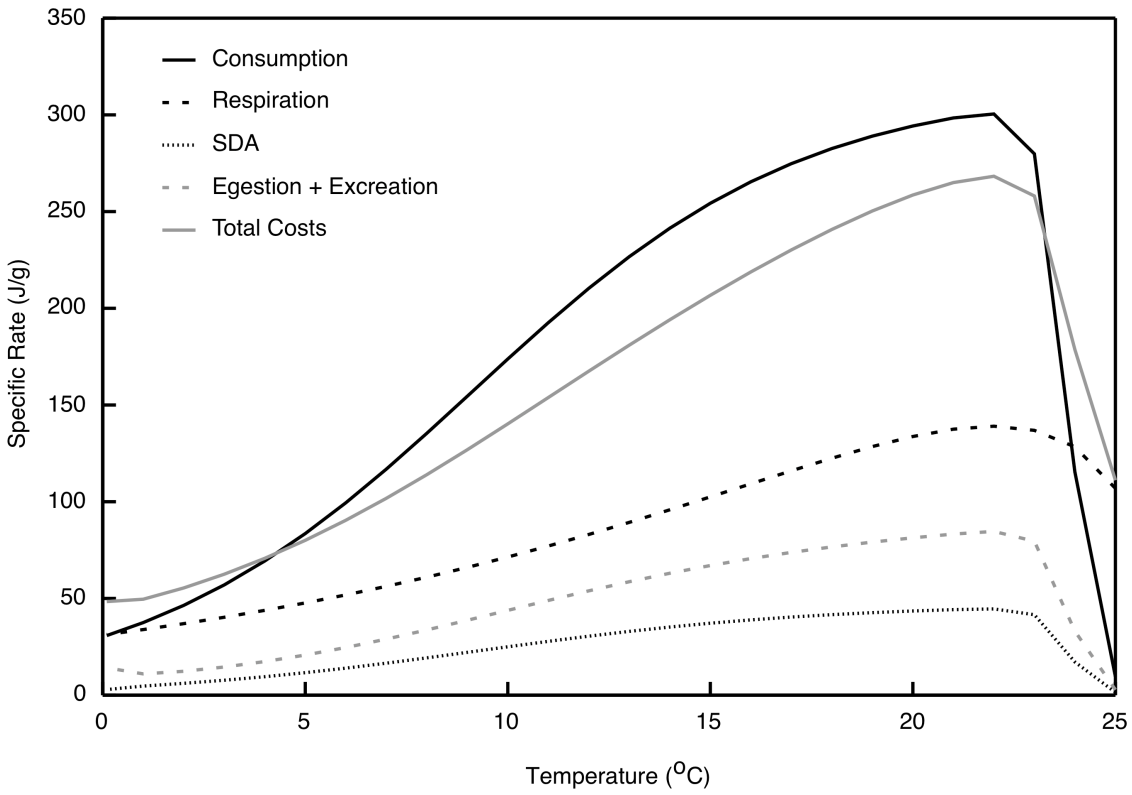

Fig. 3.1. Specific rates (J/g) for maximum consumption and metabolic costs predicted by the bioenergetics model in relation to temperature for a 10 g *O. mykiss.*

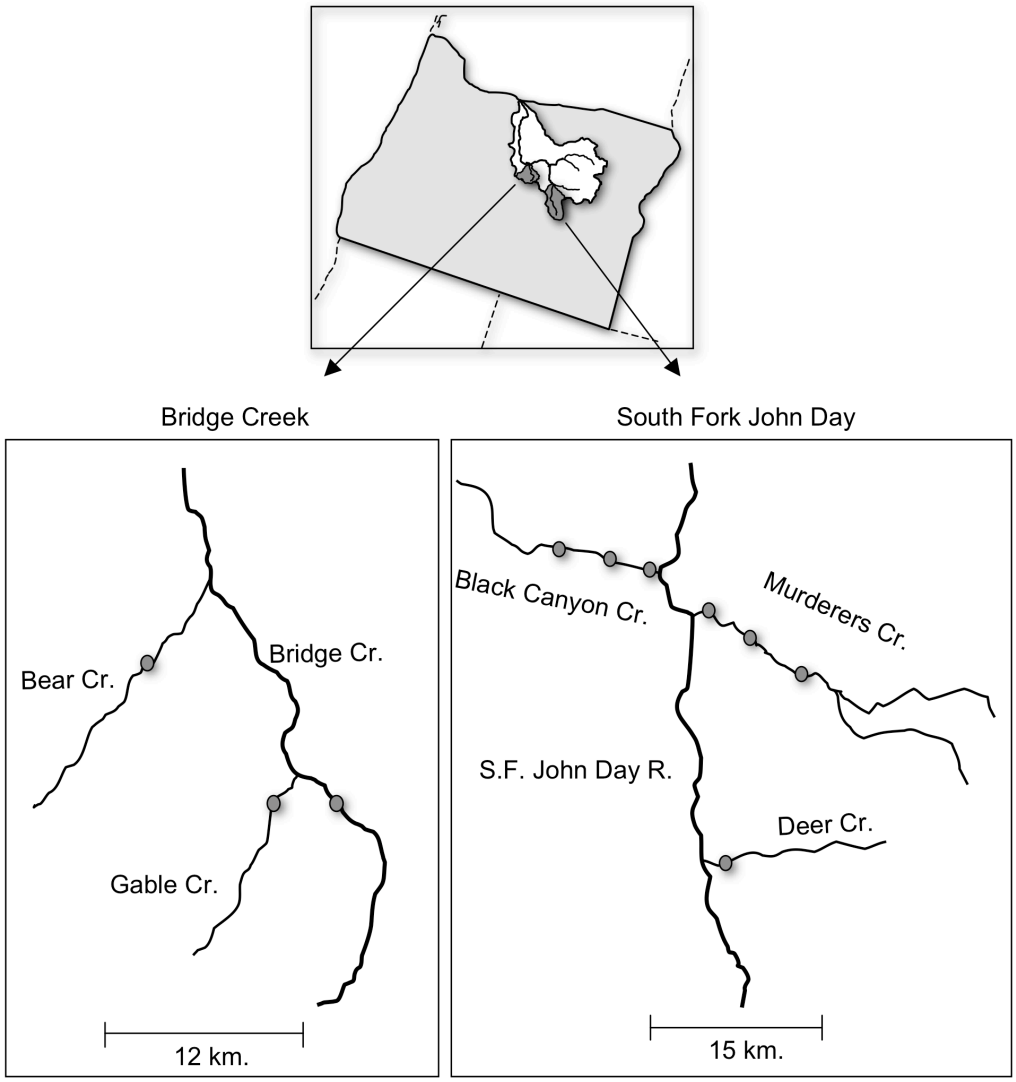

Fig. 3.2. Relative locations of the South Fork John Day and Bridge Creek sub-basins and approximate locations of each study reach (grey dots).

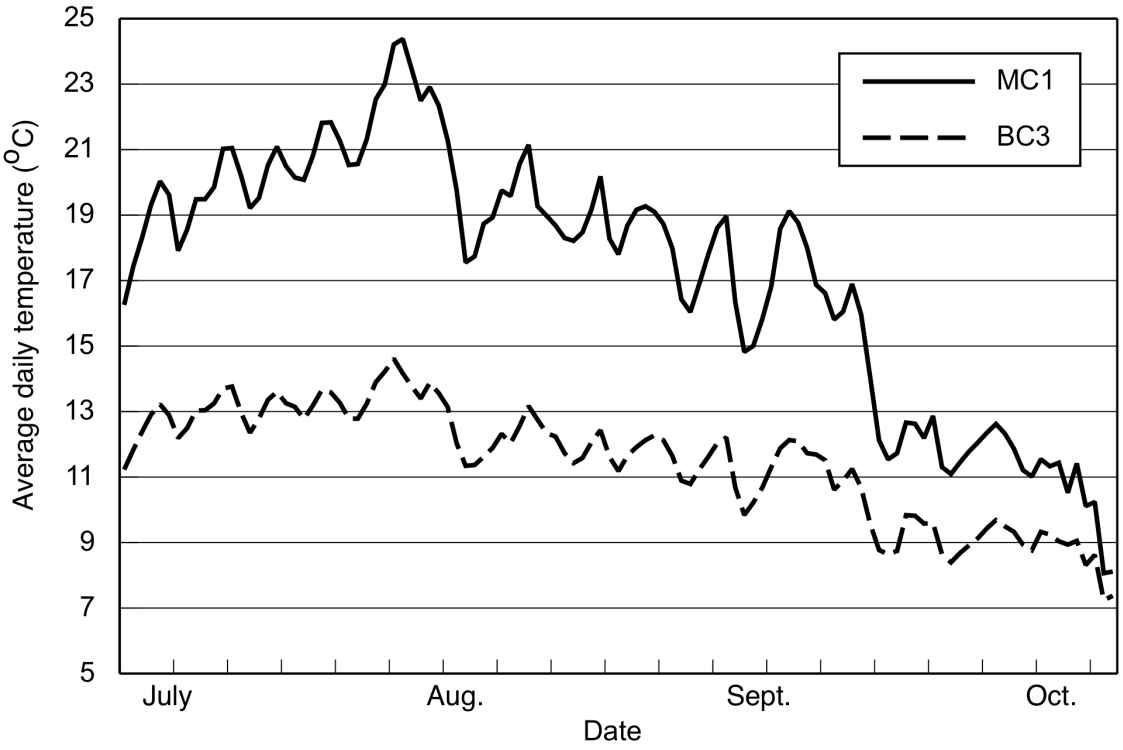

Fig. 3.3. Average daily temperature record for the warmest (MC1) and coolest (BC3) summer survey reaches, demonstrating the range of temperature encompassed within the study area.

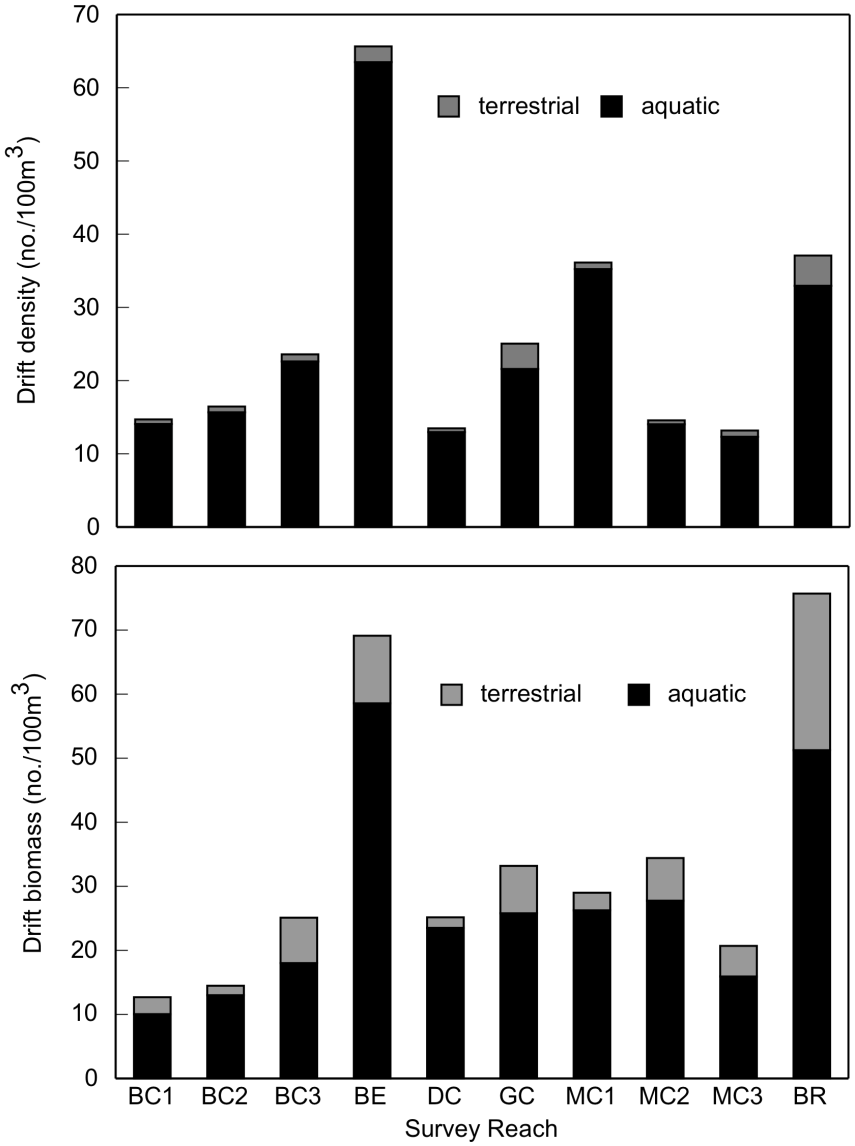

Fig. 3.4. Drift density (no./100m^3) and drift biomass (mg/100m^3) of terrestrial and aquatic invertebrates measured at each survey reach during the middle of the survey period.

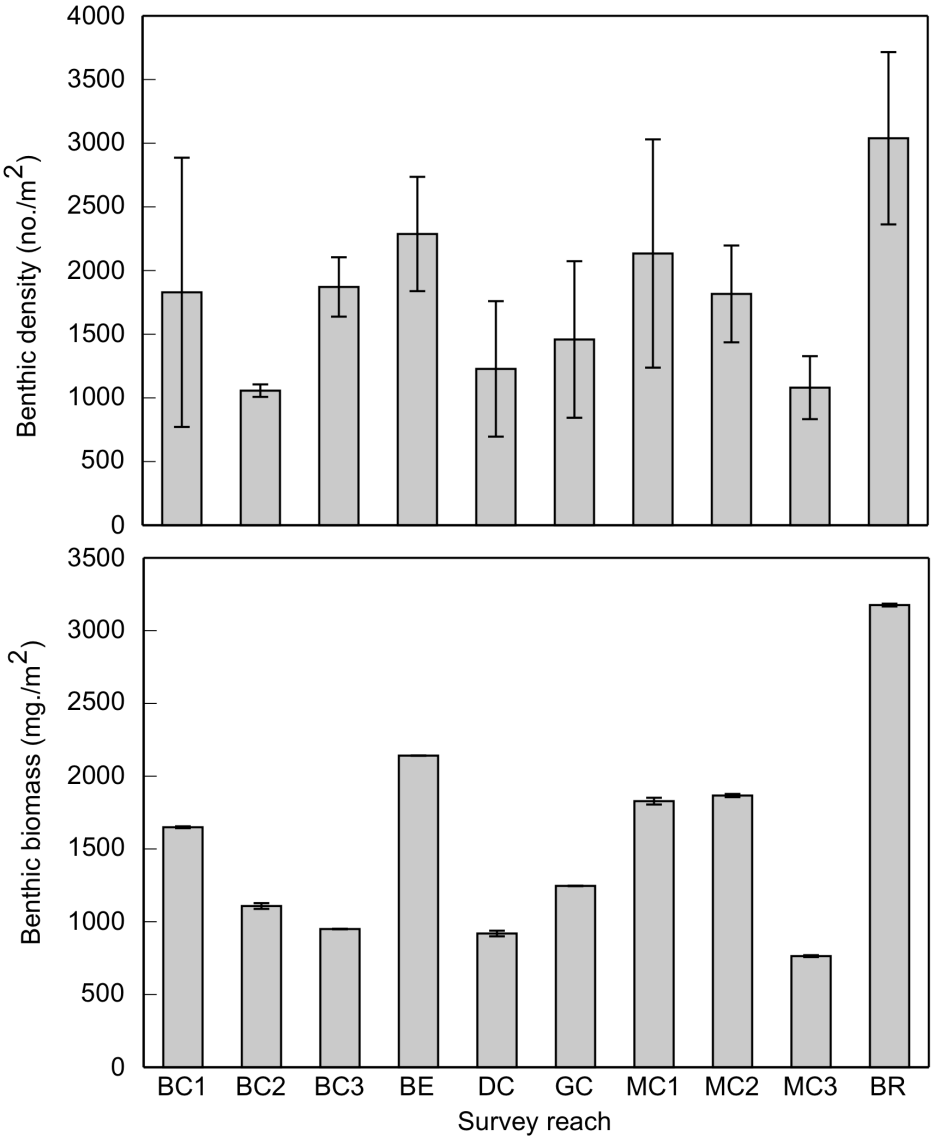

Fig. 3.5. Average (n=2) of total benthic density (no./m^2) biomass and biomass (mg/m^2) for samples collected at each of the reaches during the middle of the survey period. Error bars are one standard deviation.

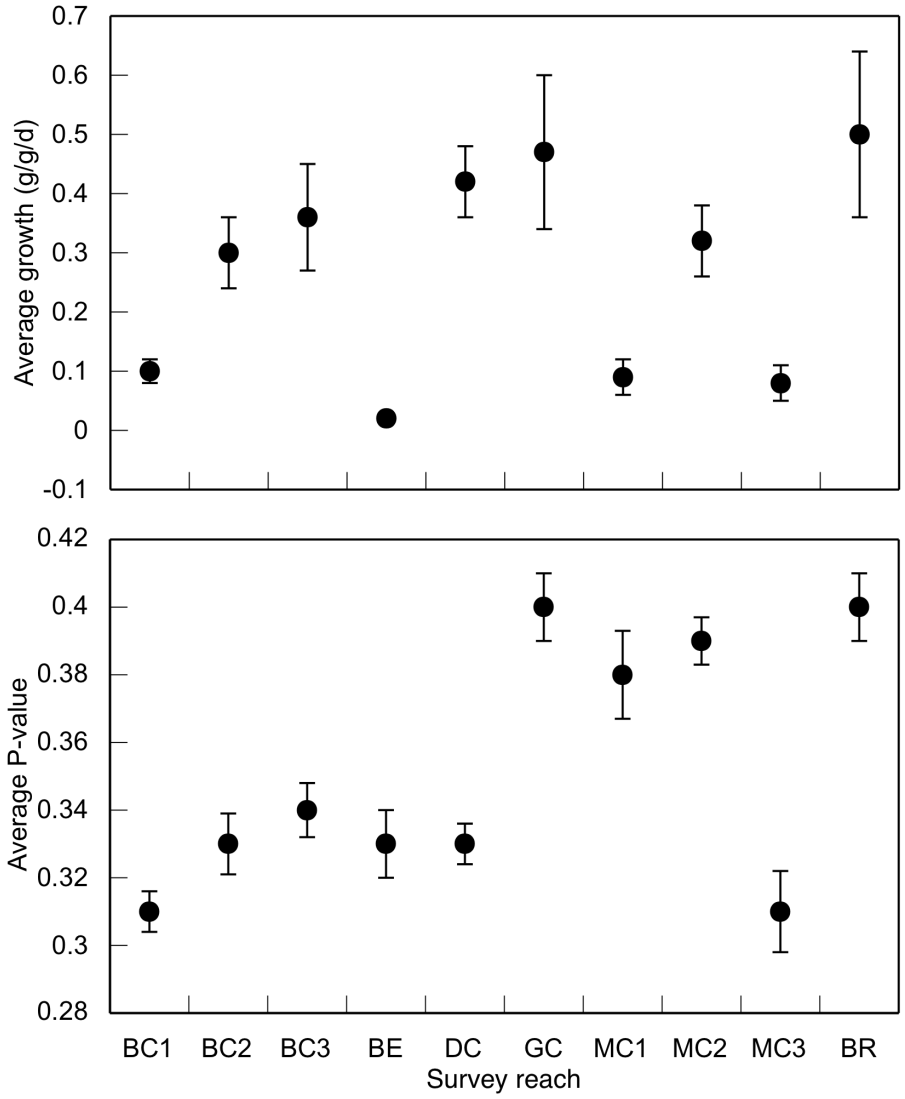

Fig. 3.6. Average of percent growth per day (%/day) and average P-values for fish in each survey reach. Error bars are one standard error.

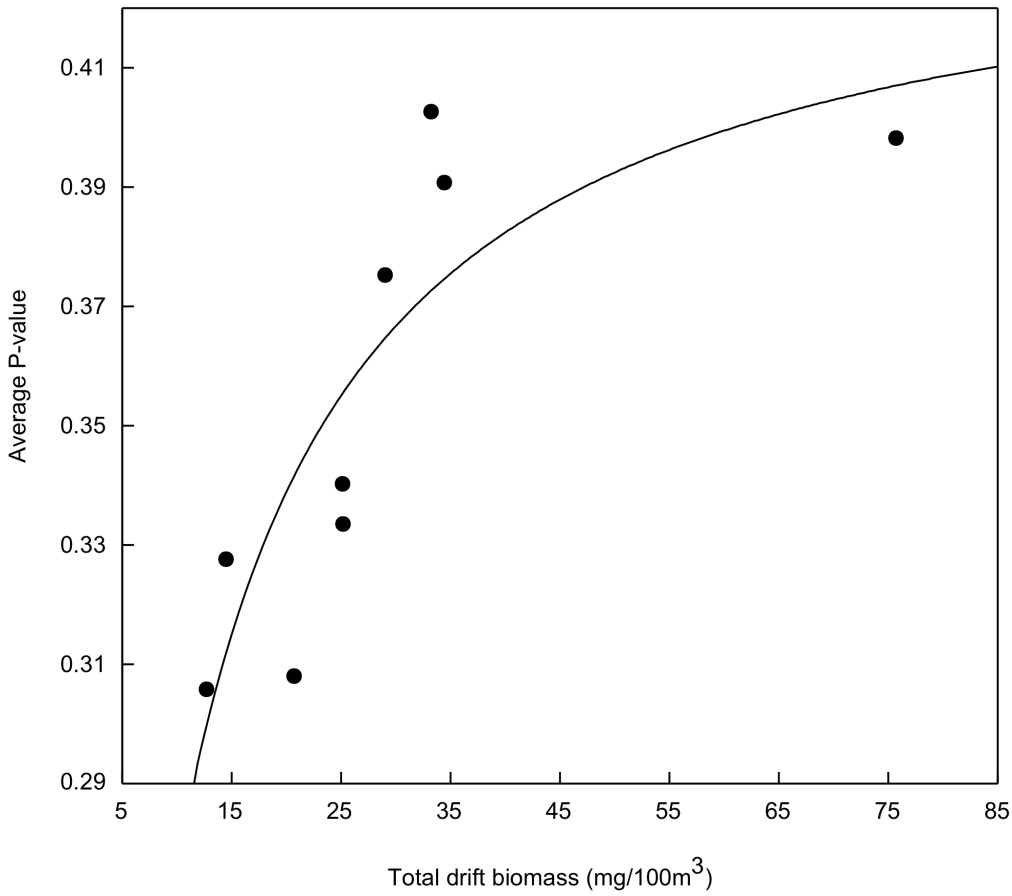

Fig. 3.7. Nonlinear regression of *O. mykiss* consumption (P-values) and total drift biomass (mg/100m^3).

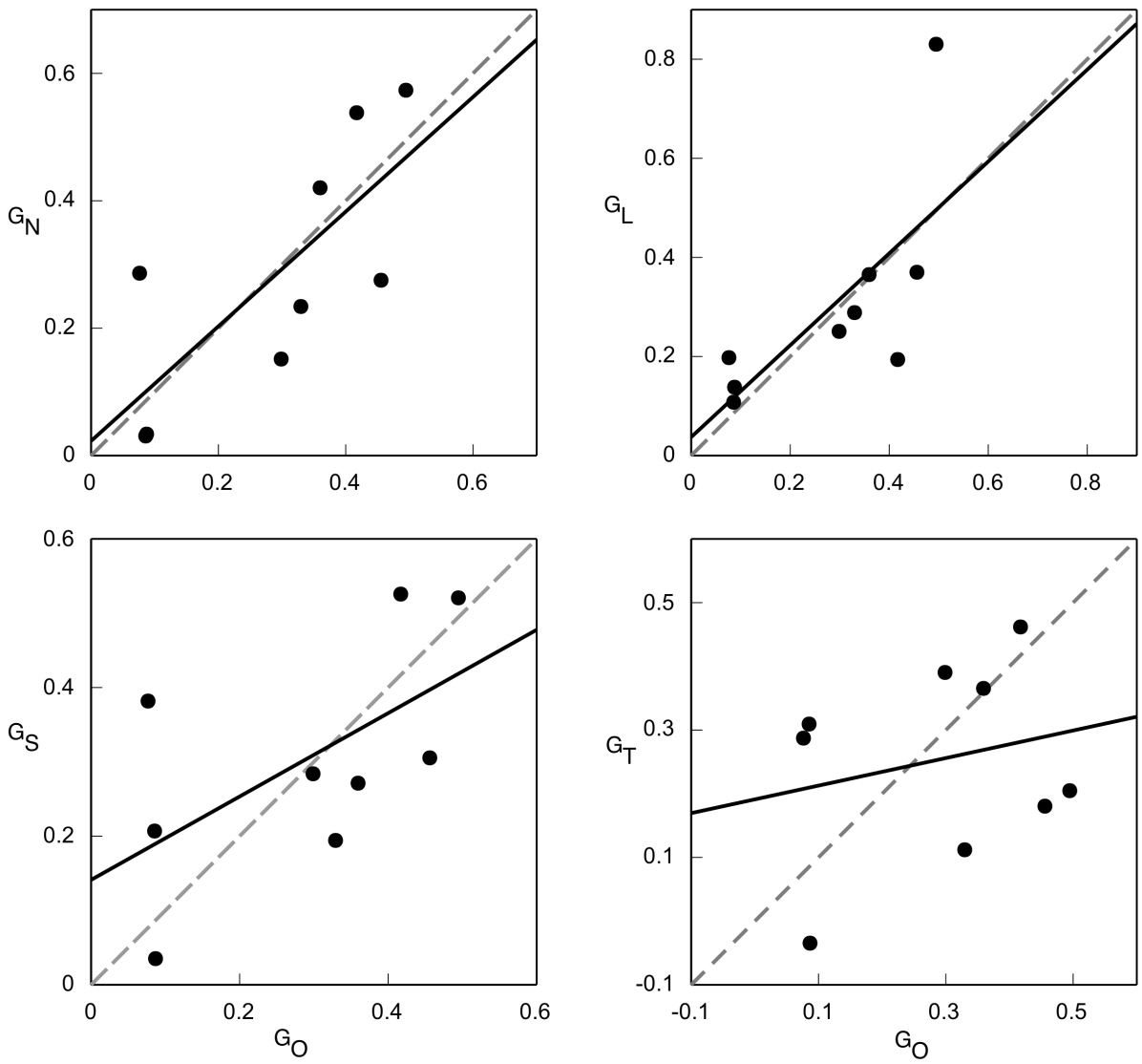

Fig. 3.8. Linear regression (solid black line) showing the agreement between observed reach averaged *O. mykiss* growth rates (GO) and growth predicted after jackknifing of best nonlinear (GN) and linear (GL) models of invertebrate abundance and consumption, average growth predicted from stream averaged invertebrate abundances (GS), and from temperature alone (GT). One-to-one line (dashed grey line) is included as a reference for equal observed and predicted growth rates.

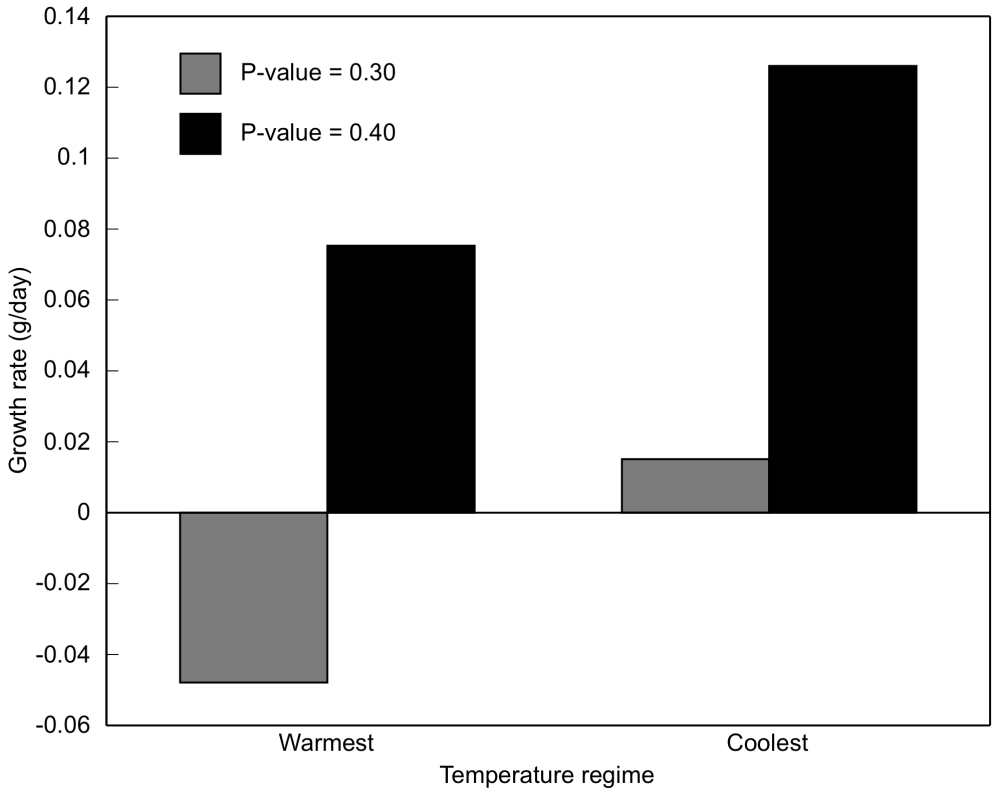

Fig. 3.9. Growth rate (g/day) for a 25 g *O. mykiss* predicted by the bioenergetics model using the lowest (P-value = 0.30) and highest (P-value = 0.40) observed average consumption values under the temperature regimes at the warmest (MC1) and coolest (BC3) survey reaches.

CHAPTER 4

CONCLUSION

To sum up, I would like to offer a short discussion of how my thesis research has contributed to the practice of fisheries management and to the understanding of lotic salmonid-habitat interactions. In doing so, I would also like to discuss aspects of my thesis research study design that can provide a template for the design of effective and informative research projects.

One of the benefits of this research project was simply its focus on making a seldom evaluated, somewhat inaccessible component of lotic salmonid environments more accessible to fisheries researchers and managers. A report by Fausch and others (1988) provides an example of how fisheries researchers have neglected the assessment of macroinvertebrate food availability as a means to explain variation in the production of freshwater fishes. In this article, ninety five mathematical models predicting fish abundances and biomass are reviewed. Of these ninety five models, only four incorporate measures of invertebrate food abundances, and the vast majority of models focus on physical habitat features (percent cover, pool area, pool frequency, etc.). In a similar article, Rosenfeld (2003) offered a more recent review of approaches used to evaluate habitat quality more specifically geared toward lotic salmonids. In this review, Rosenfeld recognizes the utility of using mechanistic, bioenergetic based models of fish growth that incorporate measures of food availability. However, he also states that the reliance on associations between salmonid abundance

and physical habitat characteristics dominates habitat assessments and models of habitat quality. It is my hope that the research described in the preceding two chapters has contributed to the growing body of research that aims to provide habitat indicators that are mechanistically linked to factors limiting the growth, abundance, and survival of lotic salmonids.

Another beneficial aspect of my thesis research project is embodied in its design. A separation often exists between those conducting pure ecological studies and those who are tasked with applying the knowledge gained through those studies to make sound decisions regarding the management of natural systems. That is to say, ecological studies may be more concerned with the identification of ecological relationships and demonstration of ecological patterns, and less concerned with the robustness of indicator metrics and the precision of sampling protocols. An exemplary aspect of my thesis research design is that equal attention was given to each of these elements.

One element of my thesis research was to determine the role of macroinvertebrate prey abundances in the regulation of salmonid growth. In light of the fact that the salmonid populations whose growth I wished to study occupied distinct stream reaches encompassing a range of temperatures, separating the influence that food consumption and stream temperature had on the expression of salmonid growth posed a difficult task. The use of a bioenergetics model that describes salmonid metabolic rates in relation to temperature allowed me to account for this temperature variation and isolate the contribution that consumed energy had on observed salmonid growth. Following

an exhaustive macroinvertebrate survey I was able to demonstrate that salmonids are able to increase their consumption rates in proportion to the amount of prey available, suggesting that food availability sets a limitation to salmonid growth. However, my thesis research did not conclude at the documentation of an ecological interaction.

Nested within the research that provided the necessary information to document the mechanistic relationship between temperature, food consumption, and salmonid growth was a study design capable of transforming this relationship into an accessible research and management tool. This brings me to the other, distinct yet complimentary element of my thesis research that focused specifically on protocol development. For instance, through consideration of a number of measures of invertebrate abundance, I was able to identify invertebrate drift biomass as the indicator of food availability that explained the greatest amount of variation in salmonid consumption. The utilization of a multi-scaled, spatially and temporally nested sampling approach provided a number of valuable insights describing variation in macroinvertebrate abundances. Based on this sampling design, I was able to determine that whole streams may be the most feasible and relevant spatial scale at which to evaluate food availability as it relates to salmonid populations. This approach also allowed for an evaluation of the sampling precision associated with invertebrate food availability metrics, and development of sampling methods that minimize unwanted sources of sampling noise. Finally, I demonstrated how observations of stream temperature and measurements of invertebrate food abundance can be incorporated into a

bioenergetics modeling framework to make accurate predictions of salmonid habitat growth potentials.

Thus, my thesis work was designed from the beginning to further ecological understanding, and turn this understanding into a functional tool that can be utilized by researchers and managers. I encourage others to design similar research projects that bridge the gap between purely ecological and purely applied research.

References

Fausch, K. D., C. L. Hawkes, and M. G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950-85. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Rosenfeld, J. S. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Transactions of the American Fisheries Society 132:953-968.

APPENDIX

Layout for invertebrate sample collections

Table A.1. Sampling design in which 2 h drift samples were used to describe finer temporal and spatial variation in invertebrate drift abundances.

Stream	Reach	Riffles per. reach	Days per. riffle	# of nets	Total drift samples
Murderers Cr.	1	1	1	2	2
	2	3	3	2	18
	3	1	1	2	2
Black Canyon Cr.	1	3	3	2	18
	2	1	1	2	2
	3	1	1	2	2
Deer Cr.	1	3	3	2	18
totals: 3 streams	7 reaches	1 -3 riffles	1 - 3 days		**62**

Table A.2. Sampling design utilizing 24 h drift samples to describe larger temporal and spatial variation in invertebrate drift sampling.

Stream	Reach	Dample date	Diel periods per date	# of nets	Total drift samples
Murderers Cr.	1	June	3	2	6
	1	July	3	2	6
	1	August	3	2	6
	2	June	8	2	16
	2	July	3	2	6
	2	August	3	2	6
	3	June	3	2	6
	3	July	3	2	6
	3	August	3	2	6
Black Canyon Cr.	1	June	8	2	16
	1	July	3	2	6
	1	August	3	2	6
	2	June	3	2	6
	2	July	3	2	6
	2	August	3	2	6
	3	June	3	2	6
	3	July	3	2	6
	3	August	3	2	6
Deer Cr.	1	June	8	2	16
	1	July	3	2	6
	1	August	3	2	6
Gable Cr.	1	June	-	-	-
	1	July	3	2	6
	1	August	3	2	6
Bear Cr.	1	June	-	-	-
	1	July	3	2	6
	1	August	3	2	6
Bridge Cr.	1	June	-	-	-
	1	July	3	2	6
	1	August	3	2	6
totals: 6 streams	10 reaches	1 - 3 months	3 - 8 periods		**192**

Table A.3. Sampling design for benthic invertebrate sample collections.

Stream	Reach	Riffles per reach	Dates per riffle	Total benthic samples
Murderers Cr.	1	1	2	2
	2	3	2	6
	3	1	2	2
Black Canyon Cr.	1	3	2	6
	2	1	2	2
	3	1	2	2
Deer Cr.	1	3	2	6
Gable Cr.	1	1	2	2
Bear Cr.	1	1	2	2
Bridge Cr.	1	1	2	2
totals: 6 streams	10 reaches	1 - 3 riffles	2 dates	**32**

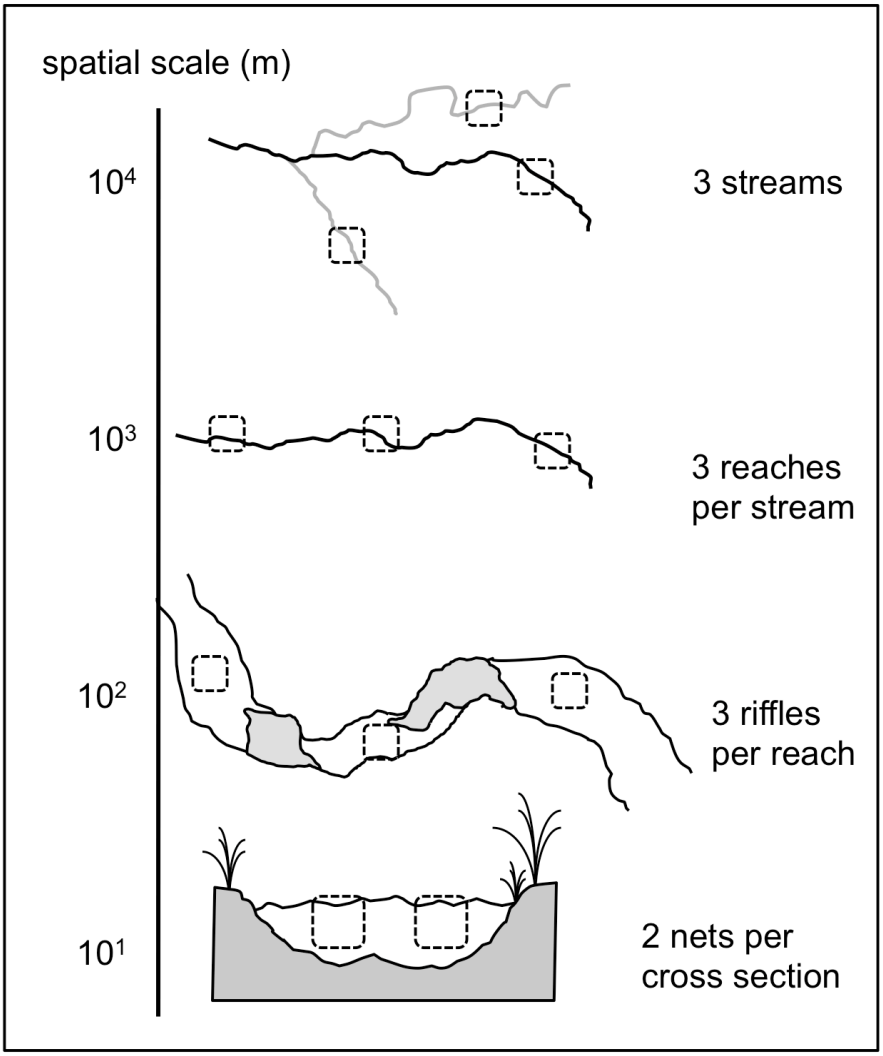

Fig. A.1. Conceptual diagram of the sampling design in which 2 h drift samples were used to describe finer spatial and temporal variation in invertebrate drift abundances. This design was repeated over 3 consecutive days on 3 reaches.

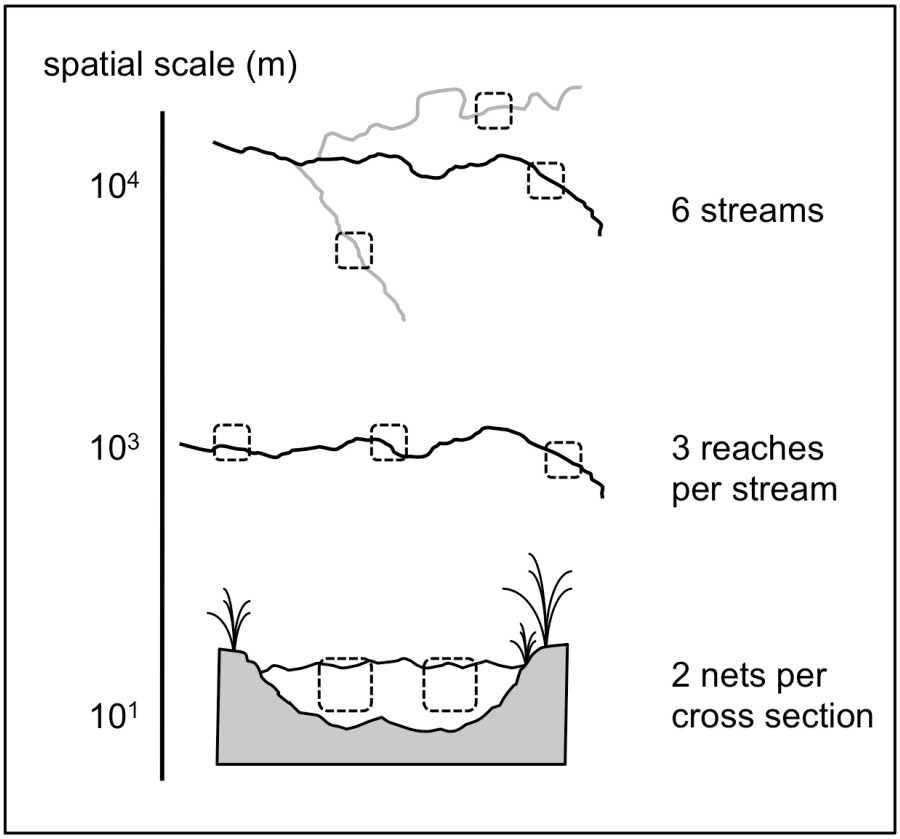

Fig. A.2. Conceptual diagram of the sampling design in which 24 h drift samples were used to describe larger spatial and temporal variation in invertebrate drift abundances. This design was repeated 3 times at several week intervals over 2 months.

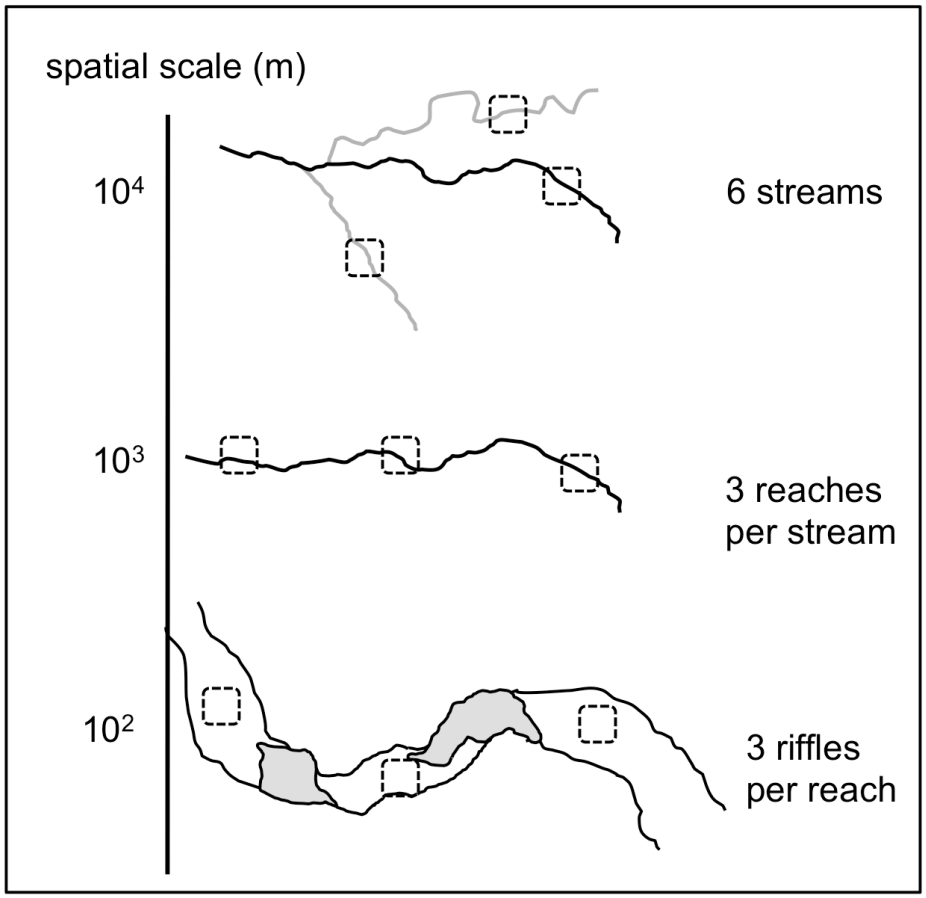

Fig. A.3. Conceptual diagram of the sampling design used to describe spatial and temporal variation in benthic invertebrate abundances. This design was repeated 2 times at intervals separated by approximately 1 month.